BREEDING BEHAVIOR AND SECONDARY SEX CHARACTERISTICS OF MALE WHITE-TAILED DEER IN SOUTHERN TEXAS

A Dissertation

by

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ABSTRACT

Breeding Behavior and Secondary Sex Characteristics of Male White-tailed Deer in Southern Texas

(December 2011)

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Environmental variation can influence forage quality and quantity which in turn can affect body condition. Body condition can affect many aspects of white-tailed deer biology, including reproduction and secondary sex characteristics. I studied male mating strategies, female reproductive success, and antler growth in southern Texas, a semi-arid environment with variable rainfall.

I captured 106 male white-tailed deer during 2006-2009, and fitted each male with a GPS radio-collar programmed to acquire locations during the rut (November to January). During peak rut, males increased movement rates, remained within home ranges except for brief excursions, and most did not conform to Levy movements. Relative to other rut phases, focal points were re-visited more often, but residency time was shortest. This behavior suggests that males may rely on spatial memory by returning to profitable areas to briefly assess female receptiveness. During drought years, such behavior was less prominent, as males were 67% more likely to remain in close proximity to a single focal point. This may be a strategy to reduce cost associated with poor body conditions during drought years.

I used 6 enclosures with supplemental nutrition and 6 without to determine influence on reproductive success. Young fed males (≤2.5 year old) sired 13% offspring while no unfed young males sired offspring. All adult females had high pregnancy rates however; mature females recruited most offspring in fed (76%) and unfed (83%) enclosures. Compared to unfed mature females, fed mature females raised more fawns (49% vs. 23%), raised more twins (31% vs. 9%), and had higher fetal counts (1.85 vs. 1.50). Supplemental nutrition allowed females to increase reproduction but did not substitute for maternal experience.

I captured 30 to 150 males annually at 7 southern Texas sites to determine repeatability of antler traits. Repeatability is the intra-class correlation between repeated measures of the same trait. Repeatability was moderate to high (0.42-0.82) for all traits. Repeatability of several traits from variable rainfall sites was lower than consistent rainfall sites. Sites with variable rainfall had 13-18% higher repeatability when feed was available. The association between repeatability and variable environmental conditions supports the role of antlers as an honest advertisement of individual condition and illustrates the magnitude of environmental influence on antler traits.

Collectively, my data improve the understanding of how the environment influences deer biology and ecology in semi-arid rangelands. The extent of environmental influences on deer was quantifiable as the availability of supplemental nutrition resulted in more consistent antler expressions and higher reproductive rates in both males and females. Lastly, the movement data improves our understanding how males search for females in an environment that can influence body condition.

DEDICATION

I dedicate this dissertation to my parents and sister who always supported my endeavors. You all played pivotal roles during my formative years. Dad, thanks for letting me tag along during hunting season when I was too young to hunt; it exposed me to nature. Mom, thanks for letting me bring home all kinds of critters; it ignited the curiosity flame. Shaina, thanks for the lengthy discussions about killing Bambi; it taught me about other peoples' perspectives.

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Movement Patterns (Chapter 1): I am grateful to King Ranch Inc. for their generosity regarding land access and project feasibility. I appreciate Dean Weimers and Dr. Tim Fulbright sharing data with me. Johanna Delgado, Jennifer Korn, and Dustin Sanders assisted with fawn captures. Mitch Lockwood and Ken Gee provided time and resources making this project possible. Dr. David Wester assisted with data analyses. I also thank the numerous deer capture volunteers from Caesar Kleberg Wildlife Research Institute (CKWRI), Texas A&M University-Kingsville, and Warnell School of Forestry and Natural Resources. Funding was provided by Texas Parks and Wildlife Department, Quality Deer Management Association, National Fish and Wildlife Foundation, King Ranch Inc., and CKWRI.

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CHAPTER I

FINE-SCALE MOVEMENT OF MALE WHITE-TAILED DEER DURING THE BREEDING SEASON IN SEMI-ARID RANGELANDS

INTRODUCTION

Male mating strategies in ungulates are influenced by the distribution of resources and the distribution of females (Langbein and Thirgood 1989). In social species of ungulates, female group sizes are large and males employ harem-defense, lekking, or resource-defense strategies to gain mating opportunities. Males compete intensely for mates, and mating success is skewed towards a small number of mature males (Clutton-Brock et al. 1988). Fighting is common and successful males are aggressive, in good physical condition, and have comparatively large antlers or horns (Hoem et al. 2007).

Most studies of male mating behavior in ungulates have been done in large-group species, as large-group species typically live in open habitats that are amenable to visual observation. Small-group species typically occupy closed habitats, and often are difficult to observe continuously. Large, cohesive social groups cannot be maintained or defended in closed habitats. Females are distributed in small groups (ca. 2 to 5 individuals), and the defense of female groups is less profitable. Males are thought to wander widely in search of estrous females (Clutton-Brock 1989).

White- tailed deer (*Odocoileus virginianus*) are a small-group species with a

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This dissertation is written in the style of the *Journal of Mammalogy*.

preference for closed habitats. The white-tailed deer mating system involves formation of tending bonds, where an individual male remains with an estrous female for 24 to 48 hours or more (Hirth 1977). Males are not territorial, but will follow the female and defend her from other males. After mating, males resume searching for additional females.

Despite differences in the mating system of large- and small-group species, it was long assumed that the distribution of male mating success was similar, where most offspring were sired by a small number of mature males (Marchinton and Hirth 1984). The recent availability of highly variable genetic markers has revealed unexpected patterns of male mating in ungulates (Coltman et al. 1999; Pemberton et al. 1992). Some species display behavioral flexibility and may alter the mating system or mating strategies in response to changes in competition, habitat, or distribution of resources (Carranza et al. 1995; Maher 1994; Thirgood et al. 1999). In white-tailed deer, mating is distributed among more males than previously expected, and immature males may breed, even in populations skewed towards mature males (DeYoung et al. 2009). Mature males are more successful on the average, but variance in mating success among individuals is lower than in lekking or harem-breeding ungulates. Surprisingly, male mating success was not correlated with antler size, which suggests that males may successfully employ mating strategies that do not rely on fighting or direct confrontation among males.

Little is known about male mating strategies in small-group species such as white-tailed deer. If defense of female groups or resources are not viable strategies, how do males locate females? Females remain dispersed in small groups through available habitat. Therefore, males that are more effective in locating estrous females may have greater reproductive success. Breeding success varies among individuals and age classes (DeYoung et al. 2009), which may reflect the use of search strategies based on previous experience or greater ability to discover estrous females. Young males are subordinate to mature males (Miller et al. 1987), which limits young males’ ability to defend females from rivals or directly challenge adult males for access to females. Consequently, young males may employ alternative tactics to locate females and gain mating opportunities (Isvaran 2005).

Finally, body condition may influence male mating effort or mating strategy. Environmental conditions prior to the rut influence forage quantity and quality, which in turn influence body condition (Mitchell et al. 1976). The rut is physically demanding, and male cervids may lose about a quarter of their body mass during the breeding season (Demarais, Miller, and Jacobson 2000; Mitchell et al. 1976). Males who enter the rut in poor body condition may be forced to limit search effort, pursue alternative tactics that require less energy, or devote additional time to eating vs. mate-searching. Prime-aged males may have an advantage because mature males can accumulate greater energy reserves than young males, who are still investing in skeletal growth. Furthermore, older individuals may invest greater effort in mating activities because they are less likely to have breeding opportunities in future years (Yoccoz et al. 2002).

The coarse spatial and temporal data derived from VHF telemetry studies limited inferences about mating behavior in a small-group species such as the white-tailed deer. The advent of global positioning system (GPS) telemetry collars has allowed researchers to analyze fine-scale movement patterns in species of large mammals (Cagnacci et al. 2010). The overall goal of this study was to use GPS locations to describe the mating strategies of male white-tailed deer during the rut. I quantified movement patterns of males during rut to determine variation in search effort and search strategy among individuals and age classes. I assumed that male movements were focused on the location of estrous females. I used *a priori* predictions to evaluate whether movement patterns were consistent with search strategies for 1) widely dispersed and unpredictable resources, or 2) dispersed, but predictable resources that could be located using prior knowledge and spatial memory. I also investigated the influence of body condition on male mating strategy.

METHODS

Study area and data collection.— My study site was located 21 km east of Kingsville, Texas in the Southern Subhumid Gulf Coastal Prairie ecoregion (EPA 2011). The property was managed for wildlife recreation, row crop agriculture, oil and gas extraction, and cattle production. Crop fields were interspersed on the north, northwest, and south-central portions of the property; crops were non-irrigated grain sorghum or cotton (gray areas on Fig. 1.1, pg. 5). The eastern portion was surrounded by bay systems of the Laguna Madre. The southern and southwestern portion was continuous brush habitat (dark areas on Fig. 1.1, pg. 5) dominated by mesquite (*Prosopis glandulosa*) and huisache (*Acacia farnesiana*). Autumn helicopter surveys during the study period indicated a sex ratio of 2-4 females per male (M. W. Hellickson, unpublished data).

During October 2005-2009, I randomly captured male white-tailed deer using the helicopter net-gunning method (Barrett et al. 1982). I estimated age based on tooth

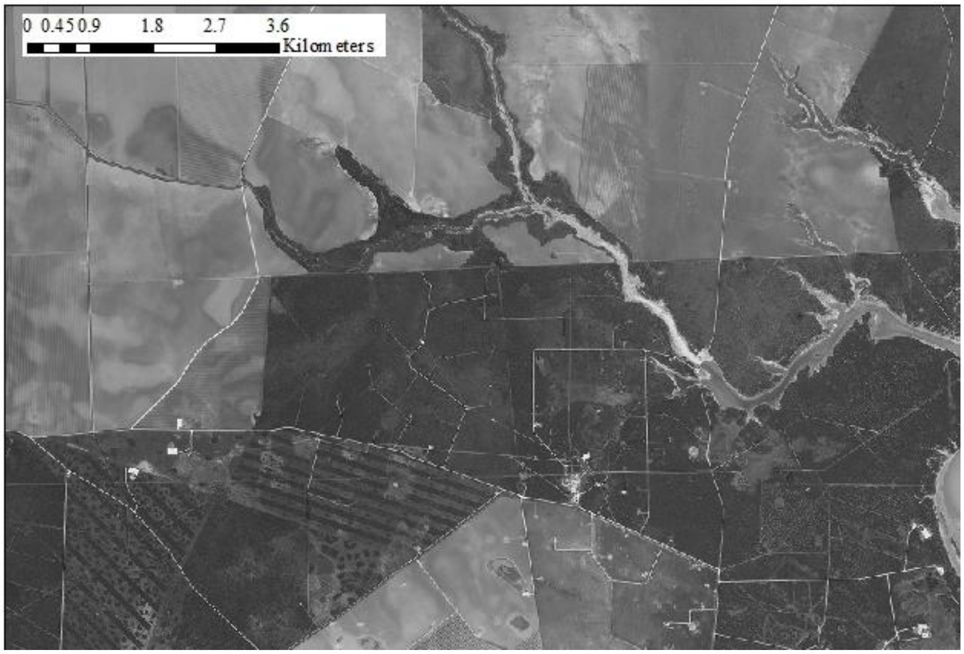

Fig. 1.1.—Aerial view of the study site in 2010. Strips and isolated patches of brush on lower left portion are the result of mechanical brush control performed during summer 2008.

replacement and wear (Severinghaus 1949). Each deer was marked with unique numbered and colored livestock ear tags and uniquely numbered passive integrated transponders (AVID, Norco, California), and fitted with a GPS telemetry collar (Advanced Telemetry Systems, Inc., Isanti, Minnesota, or Lotek Wireless, Inc., Newmarket, Ontario, Canada). I indexed body condition for males captured during 2007 to 2009. A portable ultrasound unit was used to measure thickness of rump fat for all males during 2007 to 2009. Rump fat thickness is a reliable non-invasive index of total body fat in cervids over a wide range of body condition (Cook et al. 2007; Stephenson et al. 2002).

Collars were programmed to either be remotely or automatically released in mid-February. Collars collected locations at intervals of 15, 20, or 30 minutes from the time of deployment until retrieval. Different fix schedules were chosen to allow fine-scale movement analyses, while ensuring sufficient battery life to encompass the entire breeding season. Preliminary analyses revealed that the fine-scale location intervals offered only minor advantages to movement analyses. Therefore, I used hourly locations to make all collars equal with respect to time intervals. All three-dimensional locations with position dilution of precision (PDOP) >10 and two-dimensional locations with PDOP >5 were removed, as recommended by D’Eon and Delparte (2005). I imported GPS locations into ArcMap 9.3 (ESRI, Redlands, California), and removed any apparent outliers (i.e., physically impossible locations).

I separated the breeding season into four 14-day biologically significant periods based on distribution of conception dates (Short 1970) of 146 pregnant does harvested on the study area during spring 2000 to 2009 (M. W. Hellickson, unpublished data). I defined early rut as 18 November to 1 December (14% of conceptions), peak rut as 2 to 15 December (67% of conceptions), late rut as 16 to 29 December (17% of conceptions), and post rut as 30 December to 12 January (2% of conceptions). Although breeding occurred during early and late rut, the conception dates indicated that the number of estrous females followed a bell-shaped distribution during the rut, where the greatest number of females in concurrent estrous occurred during the peak rut phase. Therefore, I could quantify male search patterns as resource availability (estrous females) changed during the rut period.

Male search effort.——Males of small-group species are thought to wander widely in search of females when resources are broadly distributed (Clutton-Brock 1989). Therefore, males who increase search effort may have an advantage in locating estrous females. Previous studies of white-tailed deer have indicated that males increase movement rates during rut, but remain within their seasonal home ranges (Hellickson et al. 2008; Webb et al. 2010). Females exist in small social groups composed of close relatives (Porter et al. 1991). The female social groups do not occupy exclusive ranges, thus females may be scattered throughout available habitats. Male home ranges probably overlap one or more female groups, but it is not known whether males search their home ranges systematically or focus their search on specific areas within their range.

I computed movement rate (m/hr) to determine if there were differences in activity among the rut phases. Missing data points may influence total distance moved; after calculating distance between each fix, I inspected each dataset for missing fixes and reset the distance measurements. For instance, if a missing fix occurred during 0900, I calculated distance from 0700 to 0800 then 1000 to 1100. Total distance was divided by available fixes.

To evaluate whether home ranges expanded in size during the rut, I used the Brownian bridge movement model (BBMM, Horne et al. 2007) to calculate 95% home ranges. Home range sizes generated by BBMM are similar to traditionally used kernel home range sizes, but BBMM enables quantification of high- and low- use portions of the range (Horne et al. 2007). I performed the BBMM analysis in R software (R Development Core Team 2008) using function *kernelbb* in package *adehabitat* (Calenge 2006).

Home range sizes may overestimate the actual area used, especially in patchy environments (Mitchell and Powell 2008). Therefore, assessment corridor (AC, Doerr and Doerr 2005) may be a more appropriate measurement to examine whether males increased search area. Assessment corridor is a technique that connects locations in a sequential order and applies a user-defined perception range to measure the actual area utilized (overlapping ACs are only measured once). I assumed a 20 m (20 m left side, 20 m right side) perception range because of the dense brush habitat. It is likely sensory perception in white-tailed deer is higher; however, my goal was to compare differences among individuals using a constant visual perception range, rather than attempt to estimate olfactory and auditory perception range, which is affected by many factors, such as wind speed and direction. Assessment corridor analysis was performed using the computer program DRAP version 0.99 (Doerr and Doerr 2005).

Search intensity, defined as the ratio of area used to home range size, may indicate whether males moved towards specific areas within their home range or traveled throughout home ranges. For each individual and rut phase, I obtained AC and divided by the 95% home range size. Low search intensity indicates that the individual focused on small areas within its home range, while high search intensity indicates that search effort was equal throughout the home range.

Male search strategy.—— An increase in male movements and search effort during the rut is plausible and consistent with previous research (Hellickson et al. 2008; Webb et al. 2010). However, the manner in which males allocate search effort may be equally important, because males who search efficiently may be more effective at locating estrous females. Whitehead (1990) predicted males should be "residents" (i.e., remain near or in a female group) if female groups are dispersed and the search or travel time between female groups is greater than duration of estrous. If travel time between female groups is short, males should use a "roving" strategy to maximize the chances of encountering an estrous female. If males use the "roving" strategy and the location of females is unpredictable, males may employ a search strategy for sparsely distributed resources, such as the Levy walk (Bartumeus et al. 2005; Viswanathan et al. 2000). However, if female locations are relatively predictable, roving males may use spatial memory and focus search efforts on areas where females are expected to occur (e.g., Gautestad and Mysterud 2005; Sueur 2011). For example, one potential strategy for roving males would be to continually re-visit females or female groups to assess receptivity.

I applied several movement analyses to determine if male movements were consistent with search strategies for resident vs. roving and unpredictable resources vs. a spatial memory and repeated visit strategy.

The Levy walk is considered to be an optimum search behavior when resources are sparsely distributed, as Levy movements increase the chances of encountering new patches within an environment (Bartumeus et al. 2002; Humphries et al. 2010; Viswanathan et al. 2000). The Levy walk is characterized by a movement path with many short movement steps interspersed with rare long steps (Bartumeus et al. 2005). In contrast, the Brownian walk is a search pattern with constant step lengths. The Brownian walk is an efficient search pattern when resources are relatively abundant (Bartumeus et al. 2002; 2005; Viswanathan et al. 1999). Use of Levy walks would imply that resources (in this case, estrous females) were distributed in an unpredictable manner. The use of Brownian walks would imply that resources were abundant, but might not determine if males had prior knowledge of female locations, or used spatial memory (Sueur 2011). Because Levy walkers have many short steps interspersed with long step lengths, the distribution of step lengths should follow a power law (Viswanathan et al. 1999). Conversely, Brownian walks consist of constant short steps, and distribution of step lengths should follow an exponential distribution (Viswanathan et al. 1999).

Although some analyses may produce spurious Levy walks (e.g., Sims, Righton, and Pitchford 2007), my analyses focused on comparisons among individuals on the same study site and temporal period. Thus, the analyses of movement strategies should provide an objective means for comparison and insights into the factors that produce the pattern. For instance, individuals that exhibit higher frequencies of long step lengths may exhibit heightened effort towards locating resources, indicating efficient search behavior or problems locating resources, depending on the context (e.g., Reynolds and Rhodes 2009). Because I had some missing fixes which could influence distribution of step lengths, I simply omitted step lengths after a missing fix from each deer’s dataset and performed a curve-fitting test (Sueur 2011) to examine whether distribution fit a power law or exponential distribution. I computed proportion of individuals exhibiting Levy walks among age classes for each rut phase. Curve-fitting tests were performed using the computer program SPSS Statistics 19 (SPSS, Inc., Chicago, Illinois).

Resources are often distributed heterogeneously across the landscape and within an individual’s home range. Home ranges generated by the BBMM algorithm are similar to the traditional kernel home range sizes (Horne et al. 2007). However the BBMM method can be used to explicitly illustrate high-use areas within the home range, termed “focal points”. During the rut, I hypothesized that focal points represent the locations of targeted resources (females or female groups). The repeated re-visitation of focal points within the home range would imply that males exhibit spatial memory for the location of females or female groups. In this context, the use of spatial memory would be an extension of the roving strategy, where spatial memory allows more efficient use of time and increases the chances of encountering estrous females. Therefore, the sizes, visitation rates, and residency time for focal points can provide insight into the profitability of the focal point, and how males respond to these focal points.

I observed several deer with unique or unusual movements, which could influence the focal point analyses. I analyzed 2 groups of individuals: those with well-defined home ranges, and those with poorly defined home ranges, including apparent dispersers, and multiple home ranges that were re-visited several times. For deer without defined home ranges during a rut phase, I provide simple movement descriptions, such as timing of movements among areas, characteristics of multiple home ranges, and home range sizes. For individuals with defined home ranges, I analyzed several patterns associated with focal points.

Output from the BBMM analyses often revealed areas where GPS locations occurred at high densities (top row in Fig. 1.2, pg. 13). Preliminary analyses revealed some occurrences where single isolated focal points were not delineated, or multiple focal points were delineated as a single focal point.

To investigate use of each focal point, I delineated each focal point using a 30% occurrence probability as a reference. I delineated exterior isopleths of each apparent focal point; if the 30% occurrence probability resulted in a single hour-glass-shaped boundary linking multiple focal points, I separated into >1 focal points. After converting locations to binary code (1 = inside focal point, 0 = outside focal point), I analyzed variables that might indicate attractiveness of focal points. First, for a focal point to be considered an attractive area, males must demonstrate a return trip (bottom row in Fig. 1.2, pg. 13). Return trips to a focal point may indicate a valuable resource was located. Some focal points were a product of a single long visit, usually during exploratory trips outside of home ranges. Therefore, I removed focal points that were visited ≤3 times.

Next, I quantified average number of focal point visits, and average duration (h) of focal point visits, measures expected to be related to profitability of the focal point. Number and duration of visits were calculated starting at when the focal point was first visited and ending at the last visit within a rut period.

I also computed number of focal points visited, which may indicate number of female groups that a male re-visited. Lastly, I calculated the spatial area of each focal

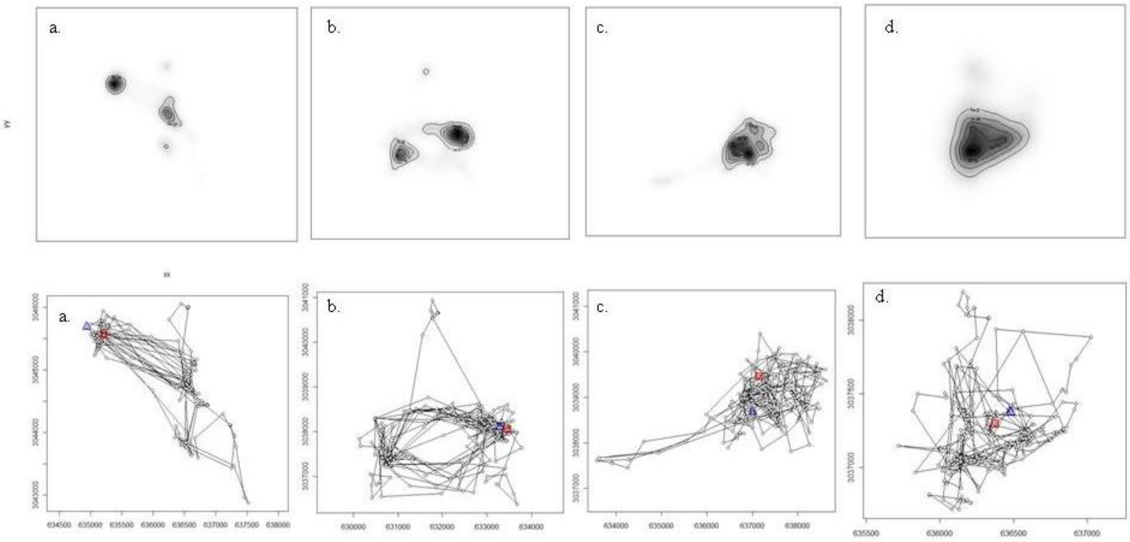

Fig. 1.2.—Brownian bridge movement model output (top row) and corresponding movement path (bottom row) of 4 male white-tailed deer during breeding season in South Texas. Two males revisited multiple focal points (a and b) and 2 males resided in a single focal point (c and d).

point. I exported all locations within each focal point and used DRAP to measure the minimum convex polygon (MCP) of each focal point.

Finally, the distribution of step lengths alone does not give insights into how an animal might incorporate spatial memory into a search for resources. Therefore, I tested for periodicities in movements among focal points as an indication of spatial memory. Additionally, if periodicity is detected, the interval between visits may give insights into male strategies. For instance, estrous lasts for 24 to 48 hours in female white-tailed deer. Therefore, the degree to which periodicity conforms to estrous duration should determine if males use the roving strategy proposed by Whitehead (1990) or if males use another strategy. I followed the approach of Li et al. (2010) and used the focal points identified by the BBMM analyses as reference points for periodicity analyses.

I applied Fourier transform (FT) and autocorrelation to detect periodicities in sequences of binary codes for each focal point. Unfortunately, both FT and autocorrelation have weaknesses; the FT is apt to generate false positives and it is difficult to establish significant thresholds in autocorrelations. Use of both FT and autocorrelation increases likelihood that observed periodicities are real (Li et al. 2010). If both FT and autocorrelation were similar (±4 hrs), I concluded the individual exhibited periodicities. I accepted ±4 hours because focal points were not clearly defined and I did not expect to remove all noise, an important consideration in FT. Periodicity analysis was performed using JMP 9.0 (SAS Institute Inc., Cary, NC).

The use of simple descriptive statistics such as Levy walks or search intensity to analyze movement patterns does not explicitly illustrate what individuals are doing throughout their movement paths (Cagnacci et al. 2010; Hebblewhite and Haydon 2010).

My analyses assume that focal points represented the location of females or female groups. To validate this assumption, I captured 5 females during autumn 2008 and fitted the females with GPS radio-collars. I used the GPS locations to investigate female movements during the breeding season and assess whether focal points of males corresponded with female locations. I also examined focal point position relative to resource distribution and to the focal points of other males.

During summer 2008, ~800 ha of my study site were mechanically treated to curtail brush encroachment (via chaining and root plowing; Whitson and Scifres 1981). Deer are attracted to the re-growth and forbs that occur after mechanical brush control (Powell and Box 1966). Therefore, I could evaluate how the change in resource abundance and distribution influenced deer use. Because males eat less during rut to focus on mating activities (Maher and Byers 1987; Miquelle 1990; Willisch and Ingold, 2007), I assumed any change in deer distribution in response to the treatment was driven by a change in habitat use of females. I examined position of overlapping focal points during 2007 to 2009 to assess whether position of focal points corresponded to resource availability. I only examined overlapping focal points of different males to determine whether males were attracted to a similar area during a period when agonistic behavior is high.

Influence of Body Condition. ––Males rely on accumulated fat for breeding activities, and may lose up to a quarter of their body weight during the rut (Demarais, Miller, and Jacobson 2000; Mitchell et al. 1976). Males may use fat to increase search effort, or males may use fat reserves to increase time allocated to mate-searching by reducing time spent foraging. Thus, male movement patterns may be influenced by body condition. Young males are physically immature and energy is devoted to lean body-mass growth rather than fat accumulation. Smaller fat reserves may place young males at a disadvantage because they could devote less effort or time to mate-searching during the breeding season. I predicted mature males would be able to use fat reserves to put forth more effort or time towards searching for females. Rump fat thickness is a reliable non-invasive index of total body fat in cervids over a wide range of body condition (Cook et al. 2007; Stephenson et al. 2002). Rump fat of all males was measured at capture using a portable ultrasound device during 2007 to 2009.

Statistical analyses.——Prior to any age-specific analyses, I used ANOVA to test for year effects in movement patterns (i.e., movement rate, home range sizes, AC, search intensity, and focal point characteristics) because South Texas experiences dramatic year-to-year variation in rainfall, which in turn influences forage quality and quantity. I used Palmer's Modified Drought Index (PDMI) during May to September (www.ncdc.noaa.gov) to illustrate environmental variability. Rainfall during May to September is important for vegetation growth necessary for deer to acquire fat reserves. If there were no statistical differences in movement patterns among years, I pooled data across years to examine the relationships between habitat type and movement patterns. My study site was mainly continuous brush surrounded by large agricultural fields; however, there was a drainage system bordered by narrow strips of brush extending through some agricultural fields. Several males used unpaved roads that traverse the agricultural fields. Movement in constricted linear spaces may influence measurements of movement patterns such as Levy walk. I calculated percent of locations for each individual during each rut phase that were in unimpeded habitat (brush and fields) and linear habitat (unpaved agricultural roads and creek), then performed linear regressions to examine whether habitat features influenced movement patterns. Because of the repeated measures aspect of my data, I used a mixed-model analyses (PROC MIXED in SAS 9.3) to analyze differences in pooled data among age classes for each rut phase while accounting for within-animal effects. I used linear regressions to examine whether rump fat thickness influenced movement patterns for each rut phase during 2007 to 2009. I also used ANOVA to evaluate differences in rump fat thickness in binomial responses (i.e., proportion of Levy walks). Due to high number of variables collected, I report statistically significant differences ($P = \leq 0.05$) or non-overlapping 95% confidence intervals (CI). Data analysis was performed using the computer program SAS 9.3 and JMP 9.0 (SAS Institute Inc. 2010).

RESULTS

I captured and fitted GPS collars to 4, 16, 30, 31, and 25 male white-tailed deer ≥1.5 year of age (overall $n = 106$) during 2005 to 2009, respectively. I also collared 5 females in 2008. I was unable to recover 4 male collars; data from 2 male collars was omitted due to poor GPS performance. For the remaining collars, data acquisition averaged 333 fixes out of 336 possible fixes for each of the 4 rut phases. I removed data for a rut phase from individuals with ≤303 fixes (<90% of possible fixes; $n = 5$). One collar failed to record locations for several days post-capture, compromising the early rut phase for that individual. Fix acquisition from 4 collars became inconsistent during the post-rut period, perhaps due to wear and tear. Five individuals died during the data collection period; three males died of natural causes and 2 were legally harvested. Mortalities were omitted only for the rut phase when mortality occurred (Table 1.1, pg.

Table 1.1.—Number of male white-tailed deer by age class with GPS data available for movement analysis during the breeding season in southern Texas during 2005-2009.

	Male age class			
Rut phase[1]	1.5	2.5	3.5+	Total
Early	8	31	62	101
Peak	8	31	61	100
Late	8	31	56	95
Post	6	31	54	91

[1] Early rut: 18 Nov to 1 Dec; peak rut: 2 to 15 Dec; late rut: 16 to 29 Dec; post rut: 30 Dec to 12 Jan.

18). I grouped deer into 3 age classes (1.5, 2.5, and ≥3.5 years of age) due to inaccuracy of the tooth wear and replacement technique for deer >3 years of age (Gee et al. 2002). Although senescent males may display different movement patterns from young or prime-aged males, only 6 males ≥6.5 years of age were collared. Mature males outnumbered young males because harvest was highly controlled and fawn recruitment was variable and associated with rainfall (M. W. Hellickson, unpublished data). Hunting activity was minimal during the study.

Male search effort.——Home range sizes for males did not differ statistically among years or habitat feature. However, home range sizes were variable among individuals and age classes (Table 1.2, pg. 20).

Assessment corridor size (ha) did not differ by year or habitat feature, but was affected by rut phase ($F_{3, 228} = 11.37$, $P = <0.001$). Assessment corridor of males of all ages was greater during peak and late rut than early and post rut (Table 1.2, pg. 20). During late rut, AC differed by age class ($F_{2, 89} = 4.24$, $P = 0.018$), and was greater in 2.5 year old and mature males (Table 1.2, pg. 20). During all 4 rut phases, order of AC in increasing size was consistent; smallest in yearlings and largest for 2.5 year olds.

Search intensity did not differ by year or habitat type, but differed by rut phase ($F_{3, 228} = 7.60$, $P = <0.001$). During peak rut, male home ranges of all ages were more thoroughly searched ($\bar{x} = 0.36$, CI = 0.33-0.39) than during early rut ($\bar{x} = 0.29$, CI = 0.26-0.32, Table 1.2, pg. 20). I observed a consistent trend for mature males to search more intensely than 2.5 year olds throughout the 4 phases (Table 1.2, pg. 20).

Table 1.2.—Measures of search effort (95% CI) by male age classes during breeding season 2005 to 2009 in southern Texas. Data based on GPS locations from each individual were pooled by age class across years.

	Male age class			
Rut phase[1]	1.5	2.5	3.5+	Average
Home range size (ha)				
Early	2174 (1126-3222)	1297 (764-1829)	924 (538-1310)	1144 (918-1370)
Peak	1389 (667-2111)	1093 (726-1460)	873 (607-1138)	984 (758-1211)
Late	896 (125-1667)	1258 (867-1650)	916 (619-1213)	1028 (796-1261)
Post	379 (-208-967)	1014 (755-1273)	740 (540-939)	811 (573-1048)
Average	1265 (858-1672)	1165 (965-1365)	866 (717-1015)	
Assessment corridor (ha)				
Early	165 (113-218)	204 (177-230)	172 (152-191)	181 (166-197)
Peak	182 (130-233)	270 (244-296)	240 (221-259)	245 (229-260)
Late	159 (103-215)	246 (218-275)	223 (202-245)	226 (210-241)
Post	117 (56-179)	189 (162-216)	182 (161-203)	180 (164-196)
Average	158 (130-187)	227 (213-242)	205 (194-215)	
Search intensity (%)				
Early	20 (10-30)	24 (19-30)	33 (29-37)	29 (26-32)
Peak	33 (23-44)	32 (27-37)	38 (34-42)	32 (29-35)
Late	31 (20-41)	30 (25-35)	34 (30-38)	36 (33-39)
Post	40 (29-51)	26 (21-31)	32 (29-36)	31 (28-34)
Average	30 (25-36)	28 (26-31)	34 (31-36)	
Rate (m/hr)				
Early	189 (138-240)	223 (197-249)	206 (187-225)	219 (193-227)
Peak	232 (176-290)	334 (306-363)	314 (293-335)	314 (297-331)
Late	182 (119-245)	296 (264-328)	274 (249-298)	273 (256-290)
Post	162 (94-231)	220 (190-250)	224 (200-247)	218 (201-236)
Average	194 (160-227)	268 (252-285)	255 (243-267)	

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[1] Early rut: 18 Nov to 1 Dec; peak rut: 2 to 15 Dec; late rut: 16 to 29 Dec; post rut: 30 Dec to 12 Jan.

Average movement rate (m/hr) did not differ by year for any age class but was influenced by habitat type during peak (t_{96} = 28.63, P = 0.019) and late rut (t_{91} = 21.96, P = 0.027). Influence of habitat type on movements was minor. For every 1% increase in linear habitat, rates increased 0.53 and 0.58 m/hr during peak and late rut, respectively.

Movement rates did not differ by rut phase in the 1.5 year old age class, but were different in 2.5 year old age class ($F_{3, 120}$ = 11.98, P = <0.01). Movement rates were 34% and 26% greater during peak and late rut than early and post rut (Table 1.2, pg. 20). Movement rates of ≥3.5 year old males also differed by rut phase ($F_{3, 228}$ = 24.09, P = <0.01); peak and late rut movement rates were 29-34% and 18-25% greater than early and post rut, respectively. Movement rates varied by age class only during peak ($F_{2, 97}$ = 4.94, P = 0.009) and late rut ($F_{2, 92}$ = 5.12, P = 0.008). In both instances, mature and 2.5 year old males had 27-39% greater movement rates than yearlings.

Male search strategy.——Few males exhibited Levy-like movements; most conformed to Brownian movements. Habitat features appeared to influence occurrence of Levy walks; fourteen percent (35 of 244 male-rut phase-year combinations) of males in continuous brush and in mixture of linear and brush habitats (8 of 58) displayed Levy-like movements, while 4% (3 of 77) of males in linear habitat showed Levy-like movements. Levy walks were more frequent during peak rut (34%) compared to 12%, 10%, and 0% during early, late, and post rut, respectively. Levy walkers were primarily 2.5 year old males during peak rut (Table 1.3, pg. 22).

Prior to analyzing focal point use, I identified 18 individuals with unique or unusual movements: 7 potential dispersers, 6 with indistinct home ranges, and 5 individuals with 2 distinct home ranges. I used the term ‘potential disperser’ because it is

Table 1.3.—Frequency of Levy walk and measures of focal point usage (95% CI) for each male white-tailed deer age class by rut phase based on GPS locations during 2005 to 2009 in southern Texas. Data were pooled across years.

	Age Class			
Rut phase[1]	1.5	2.5	3.5+	Average
Levy walk (%)				
Early	1/8 (13%)	5/33 (15%)	6/60 (10%)	12/101 (12%)
Peak	1/7 (14%)	16/31 (52%)	16/60 (27%)	33/98 (34%)
Late	0/7 (0%)	2/32 (6%)	7/55 (13%)	9/94 (10%)
Post	0/7 (0%)	0/31 (0%)	0/50 (0%)	0/88 (0%)
Average	2/22 (9%)	23/93 (25%)	27/166 (16%)	
Number of focal points revisited				
Early	1.8 (0.7-3.0)	3.0 (2.5-3.6)	2.9 (2.5-3.3)	2.9 (2.6-3.1)
Peak	2.2 (1.2-3.1)	2.3 (1.7-2.7)	2.3 (1.9-2.6)	2.3 (2.0-2.5)
Late	2.8 (1.6-4.0)	3.3 (2.8-3.8)	2.7 (2.3-3.1)	2.9 (2.6-3.2)
Post	2.5 (1.2-3.8)	2.1 (1.6-2.6)	2.4 (2.1-2.8)	2.3 (2.0-2.6)
Average	2.3 (1.7-2.9	2.7 (2.4-2.9)	2.6 (2.4-2.8)	
Number of visits				
Early	10.5 (7.6-13.3)	9.3 (8.0-10.6)	10.7 (9.7-11.7)	10.2 (9.1-11.4)
Peak	14.6 (9.0-20.2)	16.3 (13.7-18.9)	16.0 (14.1-17.9)	16.0 (14.9-17.1)
Late	10.8 (6.3-15.3)	11.3 (9.3-13.2)	13.6 (12.2-15.1)	12.7 (11.5-13.8)
Post	11.9 (7.1-16.8)	11.7 (9.8-13.6)	11.4 (10.0-12.9)	11.5 (10.4-12.7)
Average	12.0 (9.6-14.4)	12.2 (11.1-13.3)	13.0 (12.2-13.8)	
Duration of visits (hr)				
Early	11.1 (5.9-16.4)	9.0 (6.6-11.5)	9.0 (7.2-10.8)	9.2 (7.9-10.4)
Peak	11.7 (8.4-15.1)	5.5 (4.0-7.1)	6.6 (5.4-7.7)	6.6 (5.3-7.8)
Late	6.3 (2.5-10.1)	6.4 (4.7-8.0)	6.1 (4.9-7.3)	6.2 (4.9-7.6)
Post	7.2 (-1.2-15.6)	9.2 (6.0-12.5)	10.7 (8.2-13.2)	10.0 (8.7-11.4)
Average	9.4 (6.7-12.1)	7.5 (6.4-8.7)	8.0 (7.2-8.9)	
Focal point size (ha)				
Early	20.9 (1.3-40.5)	27 (16.4-34.9)	19.0 (12.3-25.6)	21.2 (15.6-26.8)
Peak	32.7 (5.4-59.9)	34.5 (21.9-47.1)	33.4 (24.3-42.4)	33.7 (28.2-39.2)
Late	8.1 (-11.0-27.1)	24.6 (16.5-32.8)	20.7 (14.5-26.8)	21.2 (15.4-27.0)

Table 1.3.—(Continued).

	Age Class			
Rut phase[1]	1.5	2.5	3.5+	Average
Post	7.7 (-16.7-32.0)	20.9 (11.6-30.3)	24.1 (17.0-31.3)	22.2 (16.3-28.1)
Average	18.7 (7.2-30.2)	26.5 (21.5-31.5)	24.5 (20.7-28.2)	
Periodicity				
Early	3/6 (50%)	14/26 (54%)	30/52 (58%)	47/84 (56%)
Peak	4/6 (67%)	14/28 (50%)	29/54 (54%)	47/88 (53%)
Late	5/5 (100%)	16/27 (59%)	27/49 (55%)	48/81 (59%)
Post	4/4 (100%)	11/27 (41%)	26/46 (57%)	41/77 (53%)
Average	16/21 (76%)	55/108 (51%)	112/201 (56%)	

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[1] Early rut: 18 Nov to 1 Dec; peak rut: 2 to 15 Dec; late rut: 16 to 29 Dec; post rut: 30 Dec to 12 Jan.

possible these individuals returned to original areas after collars were released. Four dispersal events occurred during the early rut, including one 2 days post-capture. The remaining 3 dispersals occurred during late rut. Five of 7 males that dispersed were mature, and the remaining were 1.5 and 2.5 years old. Average straight-line distance between the outside edges of 95% occurrence probability home ranges was 7.2 km, ranging from 2.7 to 14.4 km. The 6 individuals with indistinct home ranges included all age classes: 1 was 1.5, 2 were 2.5, and 3 were ≥3.5 years of age. These individuals had larger 95% home range sizes ($\bar{x}$ = 4,568 ha, range = 3,721-7,723 ha) compared to average resident home range sizes ($\bar{x}$ = 735 ha). Most (4 of 6) individuals with indistinct home ranges had wide-ranging movements during the early rut. For 2 individuals, the movement pattern continued well into the peak rut. All but one eventually settled into an established home range. I observed 5 individuals with 2 distinct home ranges. These individuals did not have distinct seasonal ranges, but re-visited at least one portion of their home range >1 time during the sampled period rather than remaining within a single home range for extended periods (i.e., a rut phase). Of the 5 males, 1 was a yearling, 3 were 2.5 year olds, and 1 was a mature male. The yearling formed a new home range 1.7 km away during peak rut then returned to his original home range during late rut. A 2.5 year old male left his home range during peak rut, remained in an area 5.6 km away until the post rut, then revisited his original home range for several days, and returned to his newer home range. Another 2.5 year old male had 2 home ranges 7.9 km apart at the opposite edges of an isolated agricultural field and traveled back and forth 8 times during the rut. The remaining 2.5 year old male twice left his established home range during late rut and travelled 2.6 km east before returning to the new area during the post rut. I classified this individual as a male with multiple home ranges instead of a disperser because he returned to his original home range, unlike the dispersers who relocated fairly quickly. The mature male had 2 home ranges 8.2 km apart at the opposite sides of an agricultural field and revisited each home range 3 times during late to post rut.

After removing non-residents, average number of focal points revisited did not differ among years or by habitat features. Average number of focal points revisited by males of all ages differed by rut phase ($F_{3, 229} = 2.9$, $P = 0.036$). Number of focal points was lower during peak rut and post rut than early rut and late rut (Table 1.3, pg. 22). Number of focal points visited did not vary by rut phase in 1.5 or 3.5 year old males, but was highest during late rut for 2.5 males ($F_{3, 105}$=5.24, $P = 0.002$). Some individuals remained within a single focal point. Proportion of males in an age class with one focal point increased from early to peak rut, then decreased during peak to late rut (Table 1.4, pg. 26).

Average focal point visitations for all age classes did not differ by year but differed by rut phase ($F_{3, 229} = 8.31$, $P = <0.001$). Visits occurred more often during peak rut than early rut, late rut, and post rut (Table 1.3, pg. 22). Habitat features influenced average number of visits during peak ($t_{86} = 16.69$, $P = 0.006$) and late rut ($t_{78} = 16.83$, $P = <0.001$). For both peak and late rut, each 1% increase in locations within linear spaces resulted in an increase of 0.06 visits. Average focal point visits were similar among age classes by rut phase, but single focal point visits were variable among individuals (Fig. 1.3, pg. 27). Mature males had 13% and 17% more visits during early and late rut, respectively, than did 2.5 year olds (Table 1.3, pg. 27).

Table 1.4.—Change in proportions of male white-tailed deer with a single focal point by age class and rut phase during the breeding season 2005 to 2009 in southern Texas.

	Age Class			
Rut phase[1]	1.5	2.5	3.5+	Average
Early	1/6 (17%)	4/27 (15%)	10/52 (19%)	15/85 (18%)
Peak	2/6 (33%)	7/28 (25%)	16/54 (30%)	25/88 (28%)
Late	1/5 (20%)	3/27 (11%)	7/48 (15%)	11/80 (14%)
Post	0/4 (0%)	12/27 (44%)	13/46 (28%)	25/77 (32%)

[1] Early rut: 18 Nov to 1 Dec; peak rut: 2 to 15 Dec; late rut: 16 to 29 Dec; post rut: 30 Dec to 12 Jan.

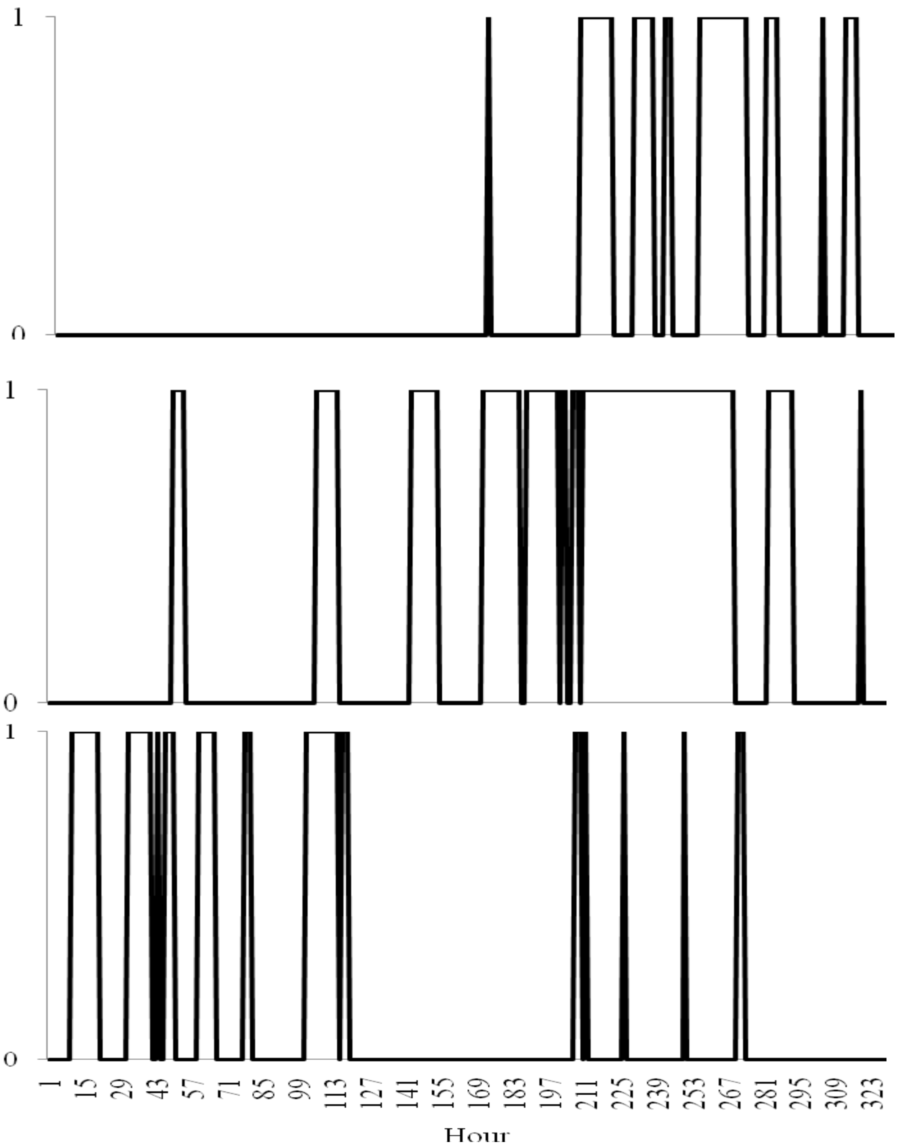

Fig. 1.3.—Differences in focal point visitation rates (1 = inside focal point, 0 = outside focal point) of a single focal point among male white-tailed deer during the breeding season in southern Texas during 2005 to 2009. Data illustrates variations in first focal point visitation, extended visits, and pauses in visitations. Males may be within another focal point when absent from illustrated focal points.

Average duration of time spent within focal point (h) during each visit did not differ among years, but varied among rut phases ($F_{3,\,228}$ = 2.63, P = 0.051). Average duration of visits for males of all ages was greater during early rut and post rut than peak rut and late rut (Table 1.3, pg. 22). There was no influence of habitat type on duration of visits within focal points. Change in duration of visits by rut phase were not different in yearlings but differed in 2.5 ($F_{3,\,105}$ = 4.25, P = 0.007) and 3.5 year olds ($F_{3,\,197}$ = 4.96, P = 0.002); visitations were shorter during peak rut and late rut than early rut and post rut (Table 1.3, pg. 22). During peak rut, yearlings spent nearly twice the amount of time ($F_{2,\,85}$ = 5.54, P = 0.006) within a focal point per visit than 2.5 and 3.5 year old males. Focal point size did not vary by year or habitat type but was ≥11 ha greater during peak rut than early, late, and post rut ($F_{3,\,228}$ = 3.32, P = 0.021; Table 1.3, pg. 22), averaged across ages and years. There were no differences in focal point size among age classes for any rut phase.

I detected periodicity in visitation of 514 focal points using FT on binary data (Fig. 1.4, pg. 29). Of the 514 occurrences, 311 (61%) corresponded with the autocorrelation results. Forty-nine to 60% of individuals exhibited periodicities, but the proportion of individuals with periodicity did not vary among years. During early, peak, late, and post rut, 56% (47 of 84), 47% (41 of 88), 41% (33 of 81), and 47% (36 of 77) individuals exhibited periodicity, respectively. Average periodicities did not vary among rut phases, ranging from 24.1 to 25.2 hours. Of the 311 periodicities, 65% were approximately daily (20-28 h). I observed 35 individuals with periodicities for 2 focal points (Fig. 1.5, pg. 31). For all rut phases, yearlings were more apt to exhibit periodicities (76%) than older males (51-56%). Of deer that exhibited periodicities, age

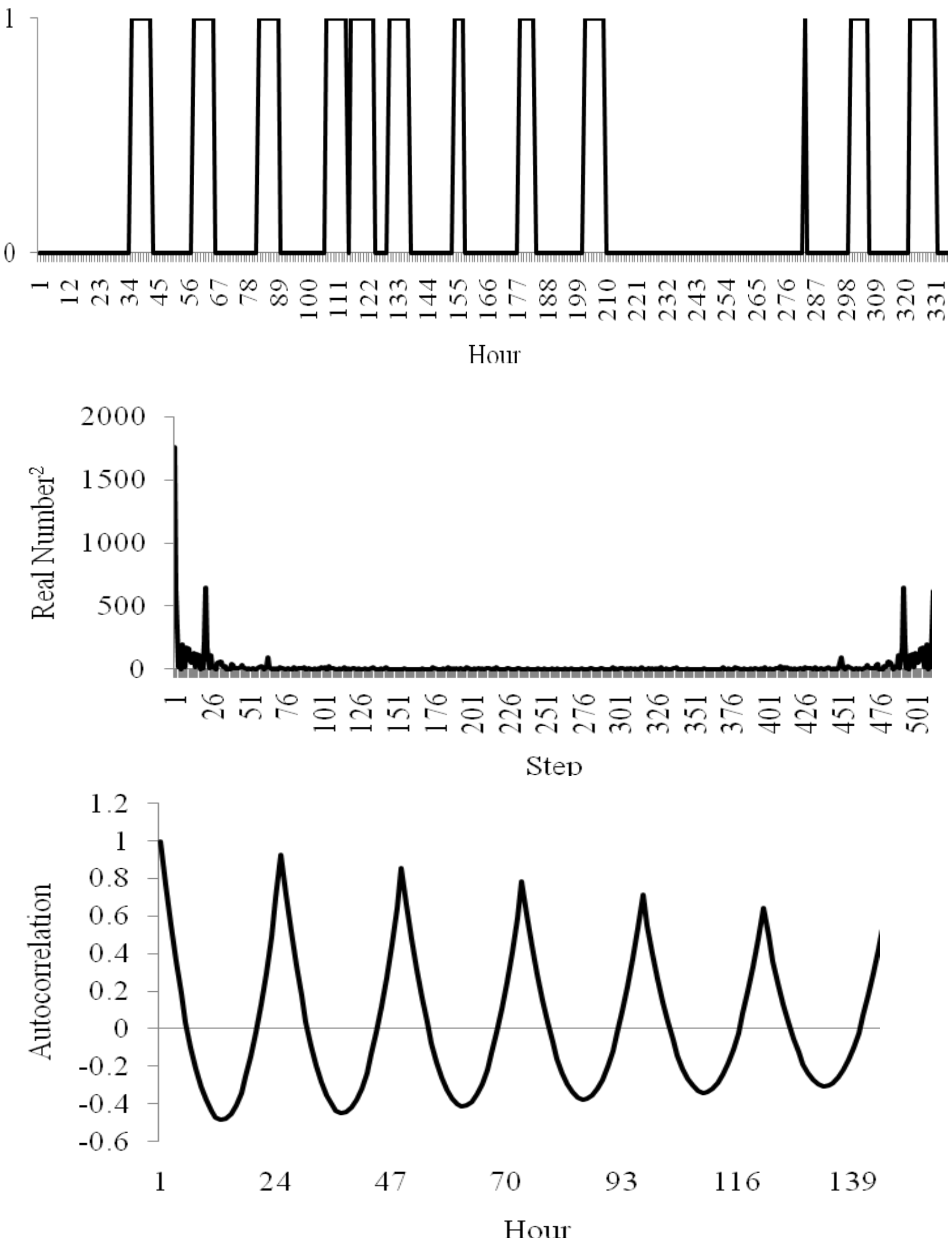

Fig. 1.4.—Illustration of a male exhibiting 24 hour periodicity. Raw binary data (top, 1 = inside focal point, 0 = outside focal point), Fourier transform periodogram (middle), and autocorrelation (bottom, right truncated for illustration purposes) of a single focal point an individual visited periodically (24 hrs) during peak rut in southern Texas. Hours between first focal point entry were 23, 24, 25,

Fig. 1.4.—(continued). —9, 15, 24, 24, 23, 81, 17, and 22 hours. Peak position in periodogram is at 22, 512 steps divided by peak position = 23.3 hours.

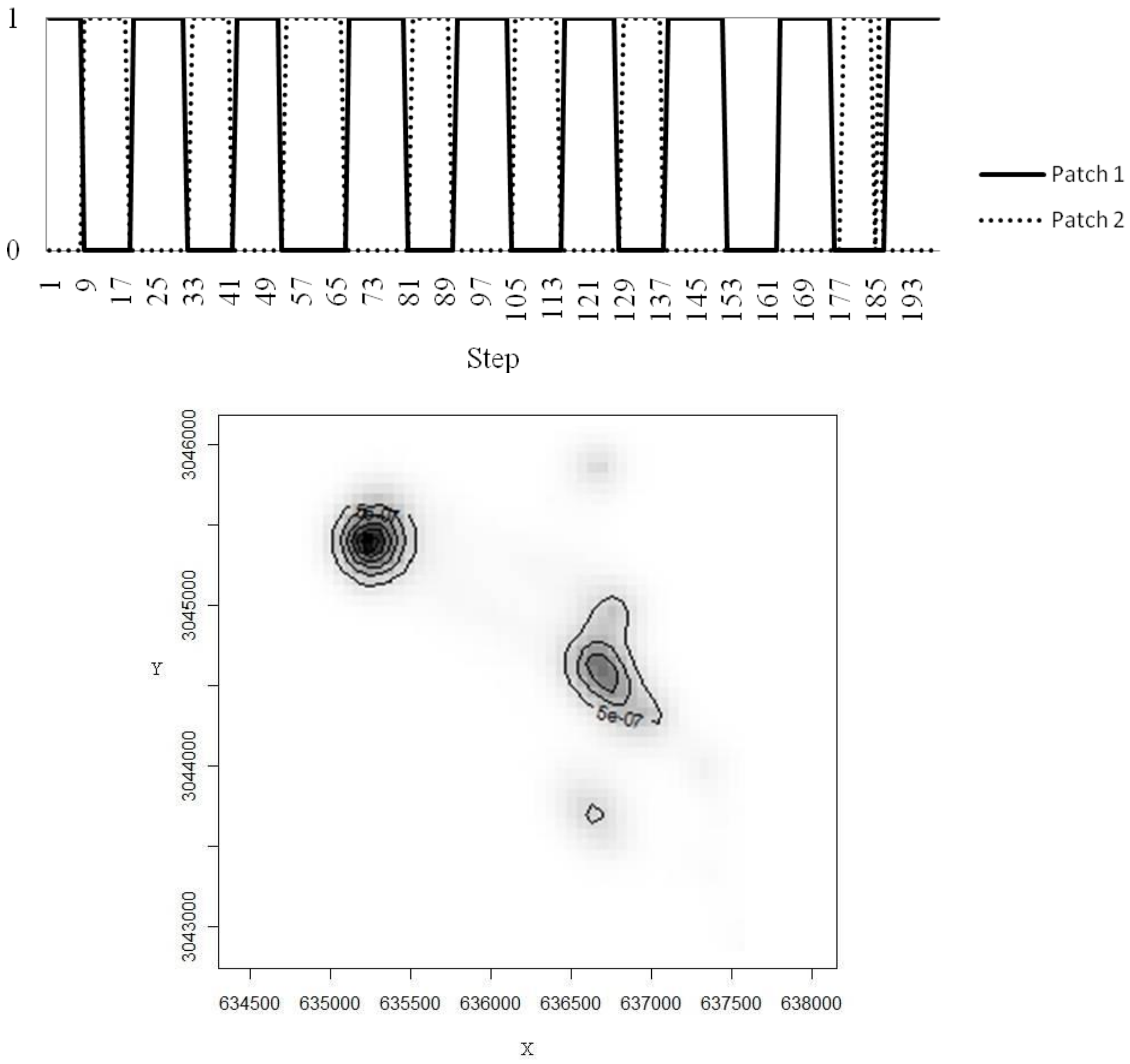

Fig. 1.5.—Raw binary data (1 = inside focal points, 0 = outside focal points) of a male white-tailed deer exhibiting periodicities between 2 isolated focal points 1.3 km apart (bottom image) in southern Texas during early rut, 2007. Data were right truncated for illustration purposes.

classes differed in the length of periodicity during peak rut ($F_{2, 44}$ = 4.34, P = 0.019). Yearlings had longer periodicities ($\bar{x}$ = 35.5 hr, 95% CI = 27.33-43.67) than 2.5 year olds ($\bar{x}$ = 21.96, 95% CI = 17.60 – 26.33). Only 20% of individuals maintained periodicities throughout all sampled rut phases.

On average, for all males focusing on a single focal point, search intensity was 12% higher, focal point size was 55% larger, AC was 20% lower, and movement rate was 14% lower than males revisiting multiple focal points (Table 1.5, pg. 33). Furthermore, number of visits, duration of visits, and number of days a focal point was visited was 31%, 50%, and 31% lower in males with a single focal point than in males with multiple focal points. Multiple focal point movements during peak rut appeared to be influenced by environmental conditions. During peak rut in 2006-2009 (dry, wet, average, and dry, respectively), proportion of individuals that focused on a single focal point was 47%, 17%, 12%, and 45%, respectively.

During 2007, 6 of 29 collared males (21%) formed 3 clusters, areas where focal points overlapped for ≥2 males, in the southwest portion of the study area (Fig. 1.6, pg. 35). Most (15 of 29, 52%) individuals clustered in the areas bordering agricultural fields. These clusters contained 2, 3, 4, 5, and 7 individual males. The interior area that would be mechanically treated for brush control in 2008 had one cluster with 6 males (21%). During autumn 2008, after brush control, there was an apparent change in position of clusters. The recently root plowed area had clusters containing twice the percentage of males (43%, 13 of

Table 1.5.—Differences in movement measures (95% CI) between male white-tailed deer visiting multiple focal points and males with one focal point by rut phase. Data were collected from GPS collars during 2005 to 2009 in southern Texas.

Rut phase[1]	N	Multiple focal points	N	One focal point
Search intensity (%)				
Early	70	30.6 (27.3-34.0)	15	35.6 (28.4-42.7)
Peak	63	34.5 (31.1-37.9)	25	44.2 (38.9-49.7)
Late	69	34.6 (31.2-37.9)	11	34.5 (26.1-43.0)
Post	51	30.1 (27.0-34.5)	25	35.5 (30.1-40.9)
Average	63	33.7 (31.0-34.4)	19	38.3 (35.1-41.4)
Focal point size (ha)				
Early	70	15.8 (10.8-20.8)	15	46.6 (35.8-57.5)
Peak	63	24.1 (16.7-31.5)	25	57.9 (46.1-69.6)
Late	69	19.7 (14.6-24.8)	11	30.7 (17.9-43.4)
Post	52	17.6 (11.1-24.1)	25	31.6 (22.2-41.0)
Average	63	19.3 (16.2-22.4)	19	43.1 (37.5-48.7)
AC (ha)				
Early	70	180 (166-193)	15	132 (103-161)
Peak	63	250 (231-269)	25	219 (190-249)
Late	69	235 (215-256)	11	184 (133-235)
Post	51	200 (180-220)	25	149 (121-178)
Average	63	217 (207-226)	19	174 (156-192)
Rate (m/hr)				
Early	70	213 (199-226)	15	163 (133-193)
Peak	63	315 (295-336)	25	299 (266-331)
Late	69	285 (263-308)	11	236 (180-293)
Post	52	238 (215-260)	25	187 (155-219)
Average	63	263 (251-274)	19	226 (206-246)

Table 1.5.—(Continued).

Rut phase[1]	N	Multiple focal points	N	One focal point
Average focal point visits				
Early	70	9.6 (8.8-10.3)	15	13.5 (11.8-15.1)
Peak	63	14.1 (12.5-15.6)	25	20.9 (18.5-23.4)
Late	69	12.2 (11.0-13.4)	11	15.4 (12.3-18.4)
Post	52	10.1 (8.9-11.3)	25	14.5 (12.8-16.3)
Average	63	11.5 (10.9-12.2)	19	16.6 (15.4-17.7)
Average visit duration (hr)				
Early	70	7.5 (6.2-8.7)	15	17.1 (14.4-19.8)
Peak	63	5.4 (4.4-6.3)	25	9.6 (8.1-11.2)
Late	69	5.4 (4.6-6.3)	11	11.2 (9.0-13.4)
Post	52	7.8 (5.7-10.0)	25	14.6 (11.5-17.7)
Average	63	6.5 (5.8-7.2)	19	13.0 (11.7-14.2)

[1] Early rut: 18 Nov to 1 Dec; peak rut: 2 to 15 Dec; late rut: 16 to 29 Dec; post rut: 30 Dec to 12 Jan.

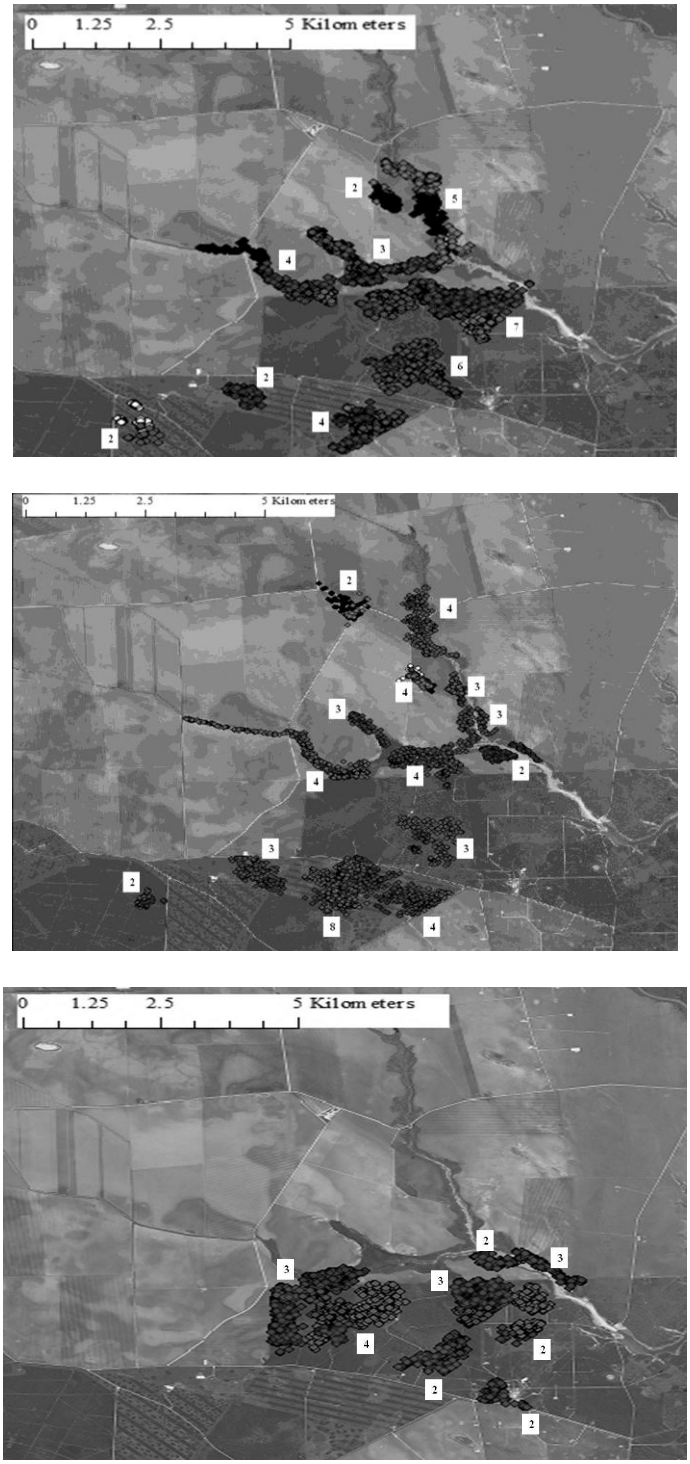

Fig. 1.6.—Overlapping male white-tailed deer focal points during peak rut, 2007 to 2009 (top to bottom) in southern Texas. Numbers in text box indicate number of males within each cluster.

30) as the previous year. Clusters were used by 2, 3, 4, and 8 individual males. The interior again only had one cluster with 3 males (10%). Areas bordering agricultural fields had 14 males (47%) in 9 clusters containing 2, 2, 3, 3, 3, 4, 4, 4, and 4 males. In 2009, there were only a few observed clusters; most focal point overlap was minimal. No clusters were observed in the mechanically treated area and only 5 (22%) bordered agricultural fields, forming 2 clusters with 2 and 3 males in each. Most individuals' focal points existed in the interior portion (50%). I observed 6 clusters with 2, 2, 2, 3, 3, and 4 individual males each.

All 3 mature females had one focal point throughout the 4 rut phases and occasionally had 1 or 2 brief forays (2 to 4 h) and 1 extended foray (21 h) outside of focal points (Fig. 1.7, pg. 37). The 50% core areas were small during early rut (17.3 ha), peak rut (17.3 ha), late rut (14.9 ha), and post rut (23.6 ha). Both young females had multiple focal points throughout the rut phases. A second small focal point of a young female was a product of several repeated visits to the same area throughout all 4 rut phases. The other young female appeared to use the mechanically treated area and a water trough about 2.3 km apart, resulting in an elongated oval home range; this individual had 2 brief forays and 1 extended foray (23 h; Fig. 1.7, pg. 37, young doe 2). Core areas of young females were larger than mature females during early rut (97.5 ha), peak rut (93.5 ha), late rut (47.3 ha), and post rut (84.1 ha). Four females decreased movement rates by 2 to 36% from early rut to peak rut, while one female slightly increased movement rates (0.8%). I assessed spatial relationship of male focal points with 4 female focal points (female with elongated oval home range and locations associated with the small focal

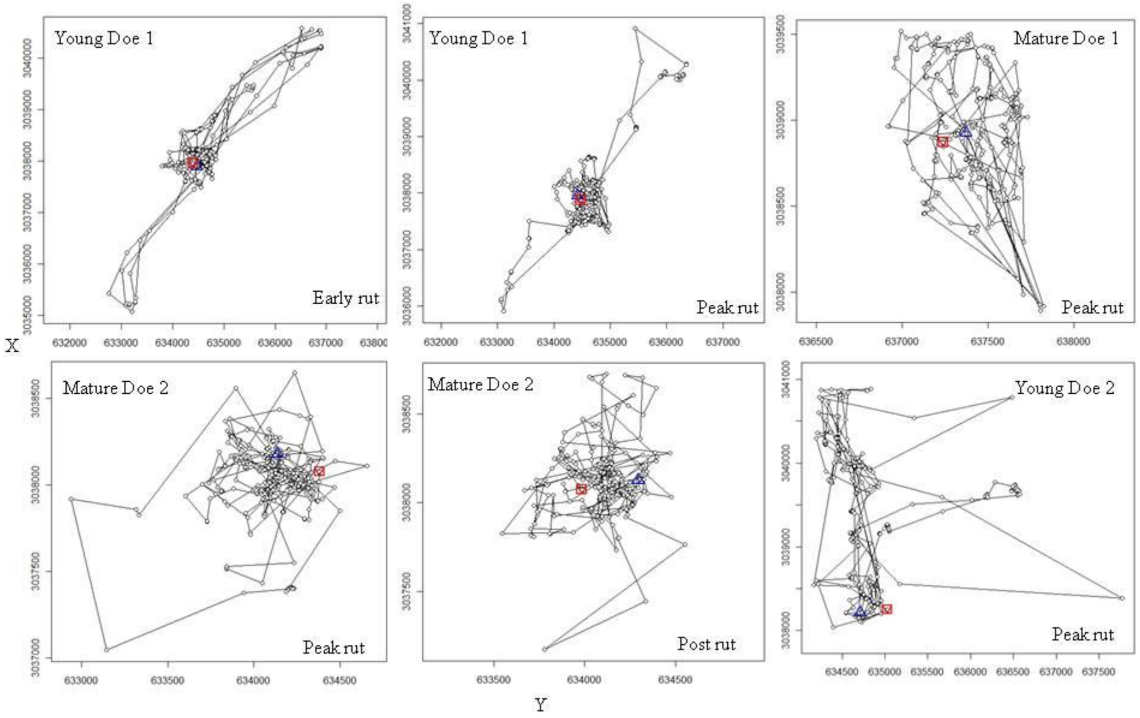

Fig. 1.7.—Selected images of female movements during the 2008 breeding season in southern Texas. Young doe 1 performed forays during peak rut however, these areas were previously visited during early rut. Mature doe 1 remained within focal point for entire duration of peak rut. Mature doe 2 performed a foray during peak rut however, some areas were re-visited during post rut. Young doe 2 performed 3 forays into areas not previously visited.

point were omitted) during peak rut; 12 of 28 (43%) collared males had a focal point overlapping or immediately adjacent to female home ranges (Fig. 1.8, pg. 39).

Influence of Body Condition.——During 2005-2009, environmental conditions were variable (Table 1.6, pg. 40). Rump fat during 2007-2009 differed among years for males of all ages ($F_{2,81} = 9.03$, $P = <0.001$, Table 1.6, pg. 40). Rump fat was 41-45% lower during 2009 than 2007 and 2008. In 2007, a wet year, rump fat was 47-60% higher in mature males than 1.5 year old males and 2.5 year old males. The same trend occurred during 2008, an average year. Mature males had 31-41% higher rump fat measurements than young males. In 2009, a drought year, there was no difference in rump fat among age classes ($F_{2,19} = 0.105$, $P = 0.90$).

I observed no relationships between movement patterns and rump fat thickness (Table 1.7, pg. 41). However, movement rates during late rut 2009 were only slightly higher than early rut (8%), whereas in 2005-2008, movement rates during late rut were 26%, 20%, 28%, and 29% higher than early rut. Reduced movement rates during late rut 2009 may have occurred due to drought conditions; five of 23 collared males died soon after the breeding season. Three of the 5 mortalities were young males, including 1 of 2 yearling males and 2 of 8 2.5 year old males. Average rump fat ($\bar{x} = 7.6$) of mortalities was 27% lower than average of all captured males in 2009 ($\bar{x} = 10.4$).

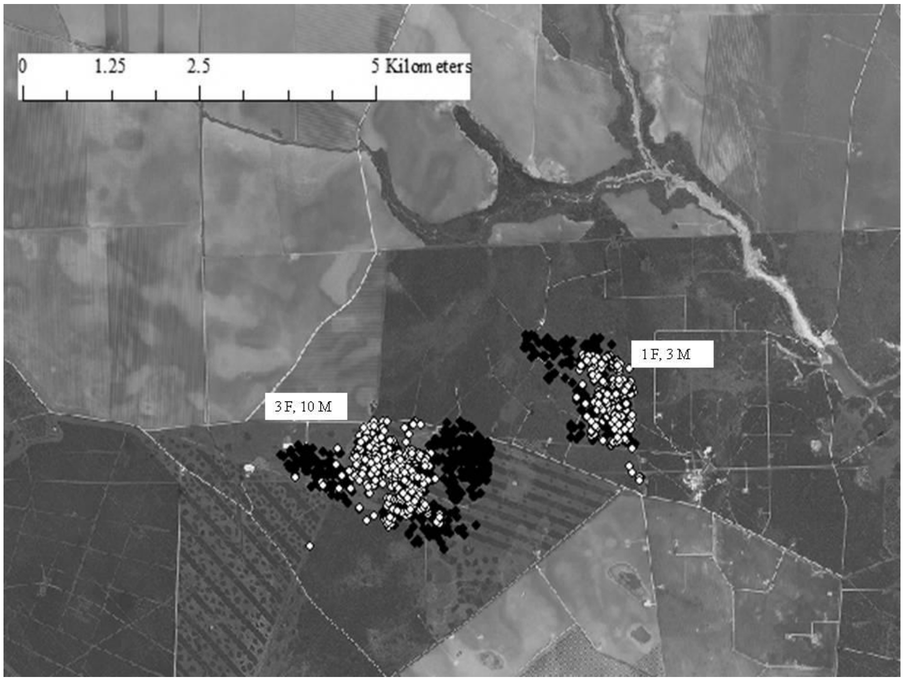

Fig. 1.8.—Male white-tailed deer focal points (black) adjacent to or overlapping female home ranges (white) during peak rut, 2008 in southern Texas. Text box indicates number of females (F) and males (M) in each cluster.

Table 1.6.—Palmer's Modified Drought Index (PDMI) during May-September and rump fat thickness (mm, SE) of 3 male white-tailed deer age classes during 2005-2009. Negative PDMI indicates a drought year.

		Age Class						
		1.5		2.5		3.5+		
Year	PDMI	N	Avg	N	Avg	N	Avg	Total Avg
2005	-0.31	-	-	-	-	-	-	-
2006	-4.57	-	-	1	23.0 (-)	4	25.5 (5.1)	25.0 (4.5)
2007	4.53	4	13.0 (5.7)	6	9.8 (3.9)	19	24.4 (7.2)	19.8 (9.0)
2008	-2.80	1	13.0 (-)	14	15.2 (4.4)	14	22.0 (6.7)	18.4 (6.5)
2009	-5.60	2	9.0 (4.2)	7	11.3 (7.5)	13	10.8 (10.8)	10.8 (6.0)

Table 1.7.—Effect of rump fat thickness on movement patterns of males with well defined home ranges from GPS data collected during breeding season in southern Texas during 2007-2009.

Rut phase[1]	Estimate[2]	DF	T-ratio	P-value
AC				
Early	-1.40	67	-1.69	0.09
Peak	0.65	70	0.62	0.53
Late	0.93	62	0.75	0.45
Post	0.68	62	0.57	0.57
All	0.29	74	0.33	0.74
Number of visits				
Early	0.09	67	0.93	0.35
Peak	-0.08	70	-1.21	0.23
Late	-0.04	62	-0.79	0.43
Post	0.05	62	0.39	0.70
All	-0.03	74	-0.76	0.45
Focal point size (ha)				
Early	0.28	67	0.79	0.43
Peak	-0.51	70	0.46	0.27
Late	-0.05	62	-0.16	0.87
Post	0.15	62	0.38	0.71
All	-0.09	74	-0.33	0.74
Rate (m/hr)				
Early	-1.47	67	-1.71	0.09
Peak	-0.21	70	-0.19	0.85
Late	0.99	62	0.68	0.50
Post	0.35	62	0.28	0.78
All	0.14	74	0.14	0.89
Intensity (%)				
Early	0.00	67	0.72	0.47
Peak	-0.00	70	-1.13	0.26
Late	0.00	62	0.64	0.52
Post	-0.00	62	-0.68	0.50
All	0.00	74	0.54	0.59

Table 1.7.—(Continued).

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[1] Early rut: 18 Nov to 1 Dec; peak rut: 2 to 15 Dec; late rut: 16 to 29 Dec; post rut: 30 Dec to 12 Jan.

[2] Change in metric for every 1 mm increase in rump fat thickness.

DISCUSSION

Male search effort.—— Male home range sizes were variable among individuals and age classes. Males increased search effort during rut as evidenced by increases in movement rate and AC during peak and late rut. Habitat type had a minor but detectable effect on movements, as males in linear habitat had higher movement rates. Males did not search widely within home ranges, as indicated by low search intensity (32-36%), nor did they leave their home ranges often. Instead, males appeared to focus activity in specific areas (i.e., focal points) within home ranges.

Male search strategy.—— Most males did not exhibit Levy-like movements but rather used a Brownian walk; most males re-visited 1 or several focal points. Visitation rates and duration of visits differed by rut phase; visitation increased and duration decreased during peak rut. Furthermore, many males displayed periodicity in movements among focal points and re-visited at intervals of 20 – 28 hours. Spatiotemporal properties of focal points provide evidence that females may be associated with the focal points. For instance, 48% of males used focal points that either overlapped or were adjacent to position of 4 collared females during peak rut. Re-visitation of areas in close proximity to female home ranges is important because of the social interaction of females. Mature females often occur in small social groups composed of daughters and granddaughters (Porter et al. 1991). Furthermore, females have short estrous periods (~24 h, ~25 d apart if not bred [Haugen 1959; Knox et al. 1988; Verme 1965]), making it difficult to predict when a particular female enters estrous. However, most females had small home ranges, implying that females or female groups might be predictably located. All mature females exhibited high site fidelity throughout the breeding season and most remained in a single small focal point. Also, focal points were visited by multiple males during a time where males are aggressive and intolerant of other males (Hirth 1977). Although the change in male focal point locations among years appeared to correspond with resource availability, males probably respond to changes in locations of females during the rut, and indirectly coincide with resource availability while tracking females (e.g. Carranza et al. 2010; Marshal et al. 2006). It is unlikely males were attracted to the resources for foraging purposes because forage intake is greatly reduced during the rut (e.g., Millesi et al. 1998). Lastly, size of focal points was similar to size of doe core home ranges. The size of focal points for males with multiple focal points was 19.7-24.1 ha which was slightly larger than female core areas (14.9-17.3 ha).

Number of males using a single focal point was influenced by rut phase, where number of males with 1 focal point increased during peak rut. This may reflect males focusing on profitable areas during peak rut or may reflect distribution of deer in the habitat as the greater number of males with 1 focal point occurred during dry years. Overall, the movements for adult males fit Whitehead's "roving" strategy; most males did not wander widely or randomly, but revisited focal points repeatedly at interval of about 24 hours. Re-visiting profitable areas may be an ideal strategy to assess receptivity of females when timing of estrus is unpredictable (e.g., Dunbar, Buckland, and Miller 1990). Males that breed with a female closest to ovulation tend to be successful (Preston, Stevenson, and Wilson 2003). Mature males may recognize estrous via a combination of female behavioral and chemical cues (DeYoung and Miller 2011), which would explain the repeated visits to presumably assess female receptiveness. The brief assessment behavior may reduce the trade-offs associated with a resident strategy (e.g., Whitehead

1990); males that spend less time waiting for a female to enter estrus will increase chances of encountering another estrous female. Many males exhibited repetitive movements among focal areas, where periodicity was about 24 hours. Periodicity may be a strategy to minimize missed opportunities to assess estrous. Re-visitation at short intervals (i.e., several hours) would be less efficient if behavioral signs of estrous do not have a rapid onset, while longer intervals between visitation (i.e., 2 to 3 days) may risk missing a female in estrous.

My results illustrate that many males appear to rely on spatial memory to re-visit and assess estrous, timing visits in an efficient manner to detect onset of estrous. It is possible that some of the single focal points may reflect a resident strategy and were used by males of all age classes. I was unable to determine if the single focal point is a response to female distribution or competition for resources.

Unique movements.— Of 100 males, 18 had movements other than within a single, well-defined home range. These movements were apparent dispersals (7%), multiple home ranges (5%), and indistinct home ranges (6%). Use of multiple home ranges was surprising, as such behavior has not been previously reported. I observed several individuals without a fixed home range during early rut that eventually settled down during peak to late rut, similar to the "wanderers" described by McCoy et al. (2005). Age did not appear to be a factor, as the wandering males ranged from 1.5 to ≥3.5 years old. Wandering movements of deer with indistinct home ranges may be a function of intraspecific competition during early rut, and then as dominant males shifted focus to females, wanderers may have settled into a fixed home range. Alternatively, wanderers may have been recent immigrants that were in the process of establishing a new home range. However, dispersers established new home ranges fairly quickly ($\bar{x}$ = 7.8 hrs, range = 2-26 hrs), suggesting wanderers may have exhibited a different type of behavior.

There may be environmental influence on large-scale movements including dispersals, multiple home ranges, and indistinct home ranges. Such movements were more common in 2007 (9 of 30, 30%) than 2006 (0 of 16), 2008 (5 of 29, 17%), and 2009 (3 of 22, 14%). The higher frequency in 2007 may be associated with the very wet year compared to other years. Males may have taken advantage of being in good body condition during a low risk year to relocate rather than during a dry year when resources were sparse (e.g., Wahlstrom and Liberg 1995; Walls et al. 2005). Conversely, wet conditions may have prompted some deer to move to different habitats; much of the area is low-lying and floods during extreme rain events. Overall, some individuals exhibited unique movements in a relatively sedentary, non-migratory herd. This observation has implications for future research regarding gene flow, disease transmission, and deer management in semi-arid rangelands.

Influence of Body Condition.—— I hypothesized that body condition would influence search effort or strategy. Environmental conditions clearly influenced body condition, as illustrated by the decline in body condition as PDMI decreased. Individual movement rates and rump fat were not correlated because movement rates were variable through rut phases, making it difficult to identify a period when males started and ended searching behavior. Furthermore, it was impossible to differentiate clustered sequential locations as a resting period or an individual moving rapidly in a small area. Males moving rapidly in a small area would undoubtedly burn more energy but I could not account for such movements. However, based on a population response, the drought conditions during 2009 resulted in early cessation of breeding activity during the late rut phase. The response demonstrates high dependency on fat reserves for search effort during the breeding season (e.g., Forsyth et al. 2005).

Even though most males (72%) revisited multiple focal points during peak rut, some males remained fixed within a single focal point, particularly during drought years (2006 and 2009). Individuals with a single focal point may be limiting breeding effort due to poor body condition as a result of drought conditions (e.g., Byers, Byers, and Dunn 2006). Alternatively, males with a single focal point may be using a different breeding strategy in response to changes in female distribution or social interactions among males. Costs associated with traveling to multiple profitable areas during drought years may outweigh potential gains (e.g., Whitehead 1990). The 37-66% increase in individuals that focused on a single focal point from early rut to peak rut suggests that males responded to a change in resource, indicating some type of breeding effort. These males may have used an alternative breeding strategy (Thirgood 1991) and positioned themselves in areas with high breeding activities and waited for opportunities (e.g., resident; Whitehead 1990). The increase was more prevalent in yearlings (48%) and 2.5 year olds (66%) than mature males (37%). Due to hierarchical social structure (Miller et al. 1987), younger males are unable to defend females from mature rivals, and thus would be more likely to use alternative mating strategies to obtain breeding opportunities. Adopting a resident behavior is consistent with findings that young males are more successful during peak rut (Chapter 2).

Lack of association between rump fat thickness and movement patterns in conjunction with the apparent strategy of focusing on profitable areas indicates that search effort may not be influenced by body condition. Instead, body condition may affect time spent towards foraging versus time spent searching for mates (e.g., Millesi et al. 1998). Male cervids lose up to 30% of body mass during the breeding season (Demarais, Miller, and Jacobson 2000; Mitchell et al. 1976). Energy expenditure due to increased movement rates during the rut, based on my GPS collar data, were only about 30% of energy released from body reserves, assuming a 6-week rut and a loss of 20% of body mass; thus the cost of reproduction is not only the increased movement rates but also the decrease in foraging time (Hewitt 2011). Mature males had greater fat reserves than young males, and presumably would invest less time towards foraging and more time towards mating activities. This may explain why mature males sire more offspring than young males (DeYoung et al. 2009). Lastly, movement rates may not necessarily be a function of body condition but rather individual personality (Dall et al. 2004; Jones et al. 2011).

Age Class Differences.——As previously mentioned, mature males sire most offspring (DeYoung et al. 2009) and breeding success may be associated with differences in movement patterns. However, due to large variation among individuals within age classes, I did not detect many differences in movement patterns among age classes. Nonetheless, I did observe trends in movement patterns among age classes. On average, during peak rut for all years, yearlings had 28% lower movement rates, 31% lower AC, and 49% longer focal point residency times than older males. Therefore, young males appear to invest less effort searching for females perhaps, by adopting a resident strategy (e.g., Whitehead 1990). Due to their lower fat reserves, re-visiting multiple focal points may be too energetically demanding (e.g., Byers, Byers, and Dunn 2006). Yearlings may be waiting until physical maturity prior to investing resources towards breeding opportunities (Forsyth et al. 2005; Yoccoz et al. 2002). Regardless, the reduced search effort displayed by young males supports observed differences in breeding success among ages in white-tailed deer (DeYoung et al. 2009).

Two year old males, on average, had 6% greater movement rates, 11% larger AC, 16% lower search intensity, and 16% shorter focal point residency times than mature males, perhaps suggesting higher investment towards breeding. Higher effort in 2.5 year old males relative to mature males was unexpected because 2.5 year old males only sire ~20% of offspring in age-structured populations (DeYoung et al. 2009). However, this "greater" effort may be a function of inability to defend females or may be attributed to behavioral inexperience. Two year old males may be unable to access profitable areas and therefore cover more area within home ranges. During peak rut, 52% of 2.5 year olds demonstrated Levy walks while only 27% mature males did so. Unfortunately, there is debate on Levy walk methodology, and analyses of the same dataset have resulted in different conclusions (Edwards et al. 2007; Viswanathan et al. 1999). Even though switching back and forth between Levy and Brownian walk is probable (Humphries et al. 2010), the higher frequencies of Levy walks in 2.5 year old males suggest these males were in an environment with sparsely distributed resources (Humphries et al. 2010). However, the prevalence of Brownian walkers in my dataset indicates resources were not necessarily sparsely distributed but rather access to resources was restricted (e.g., Reynolds and Rhodes 2009). Young males likely were more "Levyesque" than mature males because they may be faced with intersexual and intrasexual competition (Tooke and Camire 1991), preventing extended visits and frequent returns to profitable areas. Mature males outnumbered young males on the study site and would be able to displace or restrict the access of young males to estrous females.

Alternatively, females may prefer to breed with mature males (Sorin 2004). Mate choice is controversial and is difficult to demonstrate conclusively (Searcy 1982). If females are selective, female rejection of young males may explain heightened movement patterns in 2.5 year olds relative to mature males. Conversely, mate choice may be a function of mature males preferring to mate with mature females because mature females have higher recruitment rates (Mainguy et al. 2008; Mech and McRoberts 1990; Chapter 2).

Further research.— Movement data are needed from both sexes simultaneously to fully understand interactions between males and females. For instance, search effort in 2.5 year old males and mature males was similar, yet breeding success is skewed towards mature males. Furthermore, combining movement patterns with parentage analyses or estimates of conception dates could improve interpretation of tending and mating movement patterns. One of my aims was to incorporate such data; however, poor fawn recruitment rates limited meaningful comparisons in movement patterns between sires and non-sires. Across 5 years, only 12 of 106 (11%) collared males were assigned to an offspring which severely limited my inferences (Appendix 1). Combining movement analyses with parentage data and post-rut body condition will improve understanding of breeding effort and success among 2 potential breeding strategies I detected; periodic focal point re-visitations (i.e., roving) and a resident strategy.

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APPENDIX I

Measures of movement patterns among collared mature sires and presumed non-sires. Data not shown for 1.5 (no sires) and 2.5 (2 sires) year old males. Genetic parentage analyses were performed using sampled sires and offspring.

	N sires	Average (95% CI)	N non-sires	Average (95% CI)
AC (ha)				
Early	10	146 (108-184)	42	170 (194-240)
Peak	12	246 (212-281)	42	232 (209-254)
Late	11	240 (204-277)	38	217 (194-240)
Post	9	192 (152-232)	37	180 (156-204)
Search intensity (%)				
Early	10	32.2 (24.3-40.0)	42	35.8 (31.4-40.3)
Peak	12	40.0 (32.9-47.3)	42	38.4 (34.0-42.8)
Late	11	32.3 (24.8-39.9)	38	36.9 (32.2-41.5)
Post	9	33.3 (25.0-41.7)	37	34.0 (29.2-38.8)
Movement rate (m/h)				
Early	10	177 (133-222)	42	208 (185-232)
Peak	12	325 (284-365)	42	300 (278-324)
Late	11	306 (264-349)	38	264 (239-288)
Post	9	222 (175-269)	37	221 (196-246)
N focal points				
Early	10	3.4 (2.4-4.4)	42	2.8 (2.4-3.1)
Peak	12	2.8 (1.9-3.7)	42	2.1 (1.7-2.5)
Late	11	2.5 (1.6-3.5)	38	2.7 (2.3-3.1)
Post	9	2.7 (1.6-3.7)	37	2.4 (2.0-2.8)
Size of focal points (ha)				
Early	10	13.8 (3.3-24.4)	42	20.2 (11.4-29.0)
Peak	12	24.0 (13.9-34.1)	42	35.1 (26.3-43.9)
Late	11	27.3 (17.6-37.0)	38	19.8 (10.5-29.0)
Post	9	16.6 (5.5-27.8)	37	26.0 (16.6-35.4)
Average focal point visits				
Early	10	9.2 (6.4-12.0)	42	11.1 (9.4-12.8)
Peak	12	15.3 (12.8-17.9)	42	16.2 (11.5-15.1)
Late	11	14.0 (11.3-16.6)	38	13.3 (14.5-17.9)
Post	9	11.7 (8.8-14.6)	37	11.4 (9.5-13.2)
Average duration of focal point visit				
Early	10	8.8 (6.6-11.0)	42	9.1 (6.9-11.2)
Peak	12	4.8 (2.8-6.9)	42	7.0 (4.8-9.2)
Late	11	6.2 (4.1-8.3)	38	6.3 (4.0-8.6)
Post	9	9.1 (6.8-11.4)	37	11.1 (8.8-13.4)

CHAPTER II

EFFECTS OF SUPPLEMENTAL NUTRITION AND DENSITY ON WHITE-TAILED DEER REPRODUCTIVE SUCCESS IN SEMI-ARID RANGELANDS

INTRODUCTION

Factors influencing the distribution of reproductive success among individuals have implications for understanding life history patterns (Stearns 1989). In species of cervids, cost of reproduction is high for both sexes. As a result, reproductive effort generally increases with age as physical maturity is attained (DeYoung et al. 2009; Mech and McRoberts 1990). However, variation in reproductive success also may be correlated with environmental conditions through an influence on body condition (Gaillard et al. 1997; Lawrence et al. 2004).

During the breeding season, male white-tailed deer (*Odocoileus virginianus*) search for individual receptive females. A male and a receptive female form a temporary tending bond lasting 24 to 48 hrs, during which time the male will defend the female from other males. After mating, the male then resumes searching for females in estrous and will attempt to mate with as many females as possible during the 2 to 4 week rut period (Hirth 1977). Mate-searching and mate-guarding are energetically demanding (Hewitt 2011). Males may lose up to 30% of their pre-rut body mass (DeYoung and Miller 2011), and rely on accumulated fat reserves to sustain mating activities.

Environmental conditions during spring and summer affect forage quality, and may limit males' ability to store energy. Males achieve physical maturity after 4 years of age and are able to invest in the accumulation of fat reserves, whereas subadult males also must devote resources to skeletal growth. Mature males sire most offspring, yet young males collectively sire about 30% of fawns in age-structured populations (DeYoung et al. 2009; Sorin 2004). The distribution of male breeding success may be associated with male social status (DeYoung et al. 2006), population demographic factors (Mysterud et al. 2004), and alternative mating strategies (Sorin 2004). However, the influence of nutrition on distribution of male mating success is unknown.

Male investment in reproduction occurs mostly during rut. In contrast, females are solely responsible for parental care and face costs associated with pregnancy, lactation, and vigilance after fawning (Gittleman and Thompson 1988). Nutritional demands increase during the last trimester of gestation and are the greatest during peak lactation (Hewitt 2011). Females attain physical maturity at 2.5 years of age and are able to allocate maximal resources to reproduction after physical growth is completed. Doe fawns may attain sexual maturity in their first year if they are in exceptional body condition (Ozoga and Verme 1982).

It is difficult to disentangle the 2 important effects in fawn recruitment – body condition and maternal experience. Female white-tailed deer are considered income breeders rather than capital breeders. Reproduction is dependent on nutritional availability during late gestation and lactation; in semi-arid regions, fawn production is correlated with spring and summer rainfall (Ginnett and Young 2000). Because adult females have completed physical growth, adult females may be more responsive to spring and summer rainfall than young females. However, young females may be less likely to recruit offspring than mature females (Mech and McRoberts 1990) due to physical immaturity and lack of experience (Ozoga and Verme 1982). For instance, female white-tailed deer exhibit territorial behavior during fawning, and behavioral interactions may reduce recruitment rates in young females if fawning cover is limiting (Ozoga, Verme, and Bienz 1982). As deer densities increase, one might expect an increase in behavioral interactions and a decline in body condition, both of which may affect recruitment rates (McCullough 1979).

Because mature females have higher recruitment rates than young females, males may increase fitness by targeting mating efforts at mature females (Margulis 1993; Sorin 2004; Mainguy et al. 2008). Females also might benefit by mating with mature males, because longevity, ability to compete for mates, and physical characteristics such as antler or body condition, might equate to fitness. If assortative mating occurs in white-tailed deer, it has implications for fitness of both sexes, as well as mating strategies. Males that invest time courting and tending young or otherwise less productive females may have lower lifetime reproductive success than males that mate with productive mature females. Mature, socially dominant males might afford to be choosy because they could defend an estrous female from most challengers. Females could be choosy, but face a trade-off between potential benefits from mate choice versus not breeding during their first estrus cycle, thereby jeopardizing survival of late-born offspring.

Reproductive success of cervids is clearly influenced by nutrition, but specific nutritional effects are difficult to quantify in the field. Most studies have used indirect measures, such as weight loss and observed behavior, as an index of male breeding effort. Male breeding efforts may not translate into reproductive success because observed behavior or copulation does not always reflect fertilization or recruitment (Coltman et al. 1999). White-tailed deer prefer closed habitats and use the single-female tending strategy, so visual evidence of breeding effort is difficult to obtain. Few long-term studies of male or female reproductive success are available, and most occur on a single study site without the inferential power of a manipulative experiment. I used an experimental approach to study the effects of deer density and supplemental nutrition on male and female reproductive success. The study was conducted in south Texas, a semi-arid environment where variable annual rainfall (Norwine and John 2007) is associated with forage quality and fawn survival (Ginnett and Young 2000). Thus, my study was suited to assess the effects of nutrition and demographic variables on reproductive success.

I quantified reproductive success and compared the distribution of paternity and maternity at conception (fetuses) vs. recruited offspring (fawns >6 months of age). I examined whether nutrition influenced reproductive success among males. I also investigated temporal distribution of reproductive success to examine the role of competition among males. I determined influence of nutrition, deer density, and female age on conception dates and fawn recruitment rates. Finally, I used the paternity and maternity data to determine if assortative mating occurred among deer according to age class.

MATERIALS AND METHODS

Study design.— I used a replicated randomized block experimental design consisting of density (3 levels) and supplemental nutrition (supplemented and not supplemented) treatments on each of 2 ranches in south Texas. Ranch A was located in Dimmit and Maverick counties, about 15 km west of Carrizo Springs, Texas. Ranch B was located in Dimmit and Webb counties, about 15 km south of Carrizo Springs, Texas. The sites were in the Texas-Tamaulipan Thornscrub ecoregion (EPA 2010); typical woody vegetation was mesquite (*Prosopis glandulosa*), brasil (*Condalia hookeri*), and twisted acacia (*Acacia schaffneri*). Both sites averaged 45-50 cm of rainfall annually (NOAA 2010). Six 81-ha sites were enclosed by 2.4-m woven-wire fencing on each ranch during winter 2003-2004. The external fences were surrounded by outward woven-wire skirts buried underground to deter access of predators and large herbivores that may compete for forage or access to supplemental nutrition. Coyote (*Canis latrans*) numbers were reduced through trapping and aerial gunning. On each ranch, two enclosures were randomly assigned to a density treatment (target populations of 10, 25, or 40 deer/enclosure) and one enclosure in each density treatment was assigned to a feed treatment (no supplement or *ad libitum* pelleted supplement). Supplemental feed was provided using two feeders placed in the center of the enclosures. Supplemented enclosures were supplemented for entire duration of study; I did not change nutrition treatments for a particular enclosure. All enclosures had a water trough placed in the center of each enclosure as a permanent source of water.

Deer were initially present in most enclosures, as completion of the fencing trapped varying numbers of wild deer inside. During February 2004, roads in the enclosures were baited with shelled corn and observed deer were tallied. During March 2004, deer were captured in surrounding pastures using the helicopter net-gun method (DeYoung 1988) to adjust the density within each enclosure. Age estimates were determined by tooth replacement and wear (Severinghaus 1949); all captured deer were ear-tagged with unique colored and numbered livestock ear tags (Allflex USA, Inc., Dallas Fort Worth Airport, Texas, USA). A tissue sample for DNA analysis was obtained from each deer via a cattle ear-notch tool. Deer were released into enclosures until density targets were met. In 2005, I used drop-nets (Ramsey 1968) to capture deer inside of enclosures to either mark new individuals (fawns and individuals originally present in enclosures) or remove excess deer to maintain target densities. I also harvested deer to remove excess unmarked deer. I estimated age (Severinghaus 1949) and obtained tissue from each individual removed from enclosures, including fetuses from harvested females. Fetuses were measured to estimate conception dates (Short 1970). I attempted to sample unmarked candidate sires using cast antlers and carcass remains within enclosures. Beginning in 2007, deer were removed or added as needed to maintain density levels in enclosure using helicopter and net-gun. At least 3 fawns were also captured and tagged each autumn to assist in population estimates.

Population estimation.—— I estimated number of deer in each enclosure based on sightings obtained from infrared cameras (Cuddeback, Non Typical Inc., Park Falls, Wisconsin, USA; Foley 2007; Moore 2008). I used 4 to 5 cameras per enclosure, including cameras at feeders and water troughs. At least 2 weeks of unbaited camera surveys and 2 weeks of baited camera surveys were conducted every autumn and winter. During unbaited surveys, cameras were placed in areas of high deer use and rotated weekly. Baited cameras were placed over shelled corn and remained in the same location for 2 weeks; corn was replenished daily. I identified number of individual bucks based on antler characteristics (Jacobson et al. 1997), and estimated the number of fawns and does using mark-resight techniques. A detailed description of population size estimates may be found in Moore (2008).

The maintenance of precise target densities within each enclosure proved difficult; populations often were over or under target densities due to varying levels of recruitment and mortality in each enclosure. Therefore, some enclosures varied from their originally assigned density treatments (low, medium and high). I assigned populations a density treatment level annually based on population estimates from autumn camera censuses, and re-classified an enclosure for that year if necessary. Low-density enclosures contained <25 individuals, medium-density enclosures contained 25-<40 deer, and high-density enclosures contained ≥40 individuals.

DNA extraction and amplification.—— I extracted DNA from tissue samples using a commercial kit (DNeasy Tissue, QIAGEN Genomics Inc., Bothell, Washington, USA). For cast antler and bone samples, I drilled a 6.35 mm spade bit into the base of antler or bone to retrieve clean shavings and followed solid tissue protocols from Purgene® Genomic DNA Purification Kit (Gentra Systems, Minneapolis, Minnesota, USA) to extract DNA. I amplified 14 DNA microsatellite loci from a panel described by Anderson et al. (2002) and DeYoung et al. (2003). I evaluated each locus for Hardy-Weinberg equilibrium (HWE) and linkage disequilibrium (LD) using the computer program GENEPOP (Raymond and Rousset 1995); the Markov Chain parameters were 1,000 de-memorization steps, 200 batches, and 2,000 iterations. The HWE and LD estimates were done separately for each ranch because source stock originated from each ranch.

Parentage assignment.—— Hereafter I use ‘population’ as a term for an enclosure during a given year. I used the Identity Analysis function in the computer program CERVUS (Marshall et al. 1998) to remove duplicate genotypes caused by inadvertent resampling of individuals. For example, bucks may be sampled repeatedly by cast antlers in different years, or individuals may be re-sampled after loss of ear tags. Unmatched cast antlers were considered as candidate males in enclosures where found. I placed known-age individuals into cohorts and assembled pools of candidate parents for each cohort. Estimated values for percent of population sampled were based on autumn baited camera surveys. If a marked individual was not observed for 2 consecutive baited camera survey sessions, it was presumed to be dead and removed as a potential parent for subsequent years. I performed simulations (10,000 iterations) of observed allele frequencies and proportion of loci typed (estimated 1% error rate) for each population each year as a means to set the critical value for parentage assignments. I assigned parentage using ≥80% confidence threshold (Marshall et al. 1998). I also used CERVUS to estimate allelic diversity, polymorphism information content based on the expected heterozygosity (Botstein et al. 1980), and exclusion probabilities.

I assigned maternity and paternity; for dam-offspring parentage assignments, I assigned known-age fawns and yearlings to dams. Males ≥1.5 years old, unique cast antlers, and unique skulls were grouped as candidate sires for their respective year and enclosure. I only used skulls from my bone inventory because skulls provide information on gender and estimated age. I performed sire-offspring parentage analyses with and without known dams to ensure consistency in parentage assignments. In the event that a male sired ≥2 offspring with unknown dams, I used ML-relate software (Kalinowski et al. 2006) to determine if offspring were full siblings (i.e., originated from same dam); I assessed statistical significance of relationship estimates using 1,000 permutations. I grouped sires into 3 age classes (1.5, 2.5, and ≥3.5 years of age) and dams into 4 age classes (0.5, 1.5, 2.5, and ≥3.5 years of age) because accuracy of tooth-replacement and wear method is poor at ≥3.5 years old (Gee et al. 2002). Ages of individuals were adjusted accordingly for years preceding and following capture year. For instance, an individual aged 2.5 years old captured in year *x* was given an age of 1.5 in year *x*-1 and an age of 3.5 in year *x*+1. Accuracy of placing deer into specific age classes declines after 4.5 years old, and there is a tendency to under-age older deer (DeYoung 1989). However, aging biases were minimized because: 1) most deer captured in surrounding pastures to initially stock the enclosures were adults and had no previous offspring in the enclosures, and 2) most deer first captured inside of enclosures were young (≤2.5 years old). After conducting parentage assignments, I double-checked ages of parents and removed individuals with ambiguous estimated ages. For instance, if a deer was first captured as an adult and produced offspring during its young years (1.5-2.5 years old), it was removed from age class specific analyses because I could not verify its exact age.

RESULTS

Parentage analyses.——I genotyped 1,562 samples from the 12 enclosures: 1,230, 309, and 23 samples were soft tissue, cast antlers, and bone material, respectively. Of 309 cast antlers, 218 (71%) matched previously sampled males. Seventeen of 23 bone samples (74%) were assigned to a previously captured individual. Only 1 unmatched skull was available as a candidate parent. Polymorphism and exclusion probability (>0.99, Table 2.1, pg. 71) were high for each year on both study sites. Of the 1,230 tissue samples, 488 were fetuses, fawns, or yearlings that could be reliably placed into a cohort. I assigned parentage of 384 (79%) and 404 (83%) offspring to a dam and sire, respectively.

Reproductive success of males.——In the supplemented enclosures, after removing sires sampled by cast-antlers only (n = 20, 6% of total sires), known-

Table 2.1.—Descriptive statistics based on 14 DNA microsatellite loci from white-tailed deer on 2 ranches in southern Texas during 2004-2009. Smaller sample sizes during 2009 are due to fewer populations containing parentage data. H_e = expected heterozygosity, PIC = polymorphic information content, P(e) = exclusion probability, HWE/LD = Hardy Weinberg equilibrium/linkage disequilibrium.

Ranch	Year	N	Mean alleles	H_e	PIC	P(e)	HWE/LD
A	2004	187	12.50	0.80	0.78	0.999957	14/14
	2005	191	12.29	0.80	0.78	0.999957	14/14
	2006	185	12.07	0.80	0.78	0.999948	14/14
	2007	206	12.29	0.80	0.78	0.999496	14/14
	2008	213	12.29	0.80	0.78	0.999951	14/14
	2009	92	10.71	0.80	0.77	0.999925	14/14
B	2004	212	12.64	0.79	0.77	0.999918	14/14
	2005	216	12.00	0.80	0.77	0.999936	14/14
	2006	202	12.29	0.80	0.77	0.999942	14/14
	2007	222	12.21	0.80	0.77	0.999944	14/14
	2008	202	12.21	0.80	0.77	0.999940	14/14
	2009	77	10.43	0.79	0.76	0.999895	14/14

age mature males (n = 194) sired 82% of assigned fetuses (n = 55), while young males (1.5 to 2.5 years old, n = 101) sired 18% of assigned fetuses (Table 2.2, pg. 73).

The sire age structure of recruited fawns differed from the age structure based on fetus samples. Young males (n = 101) sired 12% (19 of 160) recruited fawns (Table 2.3, pg. 75) whereas mature males (n = 218) sired 88% (141 of 160) recruited fawns. In unsupplemented enclosures, 80 of 117 (68%) sampled offspring were assigned to a sire. Again, sires sampled by cast antlers only were disregarded (n = 9, 11% of total sires) and all 41 sires were in the ≥3.5 year old class. None of the 1.5 (n = 30) and 2.5 year old (n = 18) males sired offspring, respectively. Overall, individual males sired 0 to 7 litters.

The distribution of fetal conception dates revealed that mating opportunities for young males occurred mostly during peak rut; five of 7 litters sired by young males were conceived during a 2-week period when 59% of does were bred (Fig. 2.1, pg. 77). The remaining 2 conceptions occurred at the end of the breeding season. The breeding season in unsupplemented enclosures was relatively short, while supplemented enclosures had a long right-tailed distribution due to late-season conceptions (Fig. 2.2, pg. 78). Twelve of 14 (86%) conceptions occurred during 18 December to 22 January in unsupplemented enclosures, while 69% (47 of 68) of conceptions occurred in supplemented enclosures during the same period.

Table 2.2.—Recruited offspring assigned to known-age parents in supplemented enclosures. Table illustrates number of sampled known-age candidate parents available after population adjustments and number of known-age parents during 2004 to 2009 in southern Texas. Enc. = Enclosure, N = Estimated population size derived from camera surveys, O = genotyped offspring, S = singletons, T = twins, U = age unknown. Low density = <25 deer, medium density = 25 to 39 deer, high density = >40 deer.

Enc.	Year	N	O	S	T	Sires/Females/Offspring				Dams/Singletons/Twins				
Low Density						1	2	3+	U	0.5	1	2	3+	U
F2	04-05	10	4	3	1	-	-	2/2/2	1/0	1/0	-	-	2/1/0	-
F2	05-06	8	1	1	0	1/0	-	2/1/1	1/0	-	1/0	-	2/0	3/0
F2	06-07	7	2	2	0	2/0	1/1/1	3/0	-	-	-	-	-	4/1
F2	07-08	12	7	5	1	-	2/4/5	-	-	-	-	1/1/0	2/0/1	1/1/0
F2	08-09	13	4	2	1	-	-	2/3/4	-	-	1/1/0	-	3/1/1	-
F1	05-06	24	22	10	6	5/0	2/0	8/10/13	11/6/7	2/1/0	1/0	-	12/2/4	2/0/2
C5	04-05	19	4	4	0	-	-	3/0	4/4/4	2/0	2/0	-	3/1/0	3/0
C5	05-06	14	4	2	1	1/0	-	2/0	3/1/2	1/0	1/0	1/1/0	1/0/1	2/0
C5	06-07	11	2	2	0	-	1/1/0	2/1/1	-	1/0	1/0	1/0	1/1/0	-
C4	05-06	21	3	3	0	-	-	6/2/2	2/1/1	1/0	1/0	1/1/0	6/0	2/2/0
C4	08-09	19	9	7	1	3/0	1/0	5/4/5	1/1/1	-	1/0	2/2/0	7/1/1	1/1/0
Total			62	41	11	12/0	7/6/6	35/23/28	23/13/15	8/1/0	9/1/0	6/5/0	39/7/8	18/5/2

Table 2.2.—(Continued).

Enc.	Year	N	O	S	T	Sires/Females/Offspring				Dams/Singletons/Twins				
Medium Density						1	2	3+	U	0.5	1	2	3+	U
F1	07-08	38	8	4	2	8/0	2/0	10/6/8	-	3/0	-	-	6/3/2	1/0
F1	08-09	25	4	4	0	3/0	1/1/1	8/3/3	-	-	3/1/0	-	7/2/0	-
F4	04-05	32	17	13	2	5/0	5/0	15/11/12	3/1/0	-	-	2/1/0	13/5/1	2/0/1
F4	06-07	37	17	7	5	-	-	11/10/13	2/1/1	-	2/0/1	2/0	11/1/5	2/2/0
C4	04-05	25	1	1	0	-	1/0	9/0	1/0	-	1/0	1/0	4/1/0	2/0
C4	06-07	34	12	4	4	3/4/4	-	5/2/2	2/3/3	-	-	2/0	7/1/3	2/1/1
C4	07-08	35	9	5	2	2/2/2	3/1/1	4/3/4	1/1/1	1/0	1/1/0	-	8/1/1	1/0/1
C6	06-07	31	19	11	4	1/0	1/0	12/14/17	1/1/2	1/0	-	-	18/7/4	-
Total			87	49	19	22/6/6	13/2/2	74/49/59	10/7/7	5/0	7/2/1	7/1/0	74/21/16	10/3/3
High Density														
F1	04-05	78	15	11	2	2/0	2/0	8/6/6	15/7/7	2/0	4/1/1	1/0	19/4/1	7/2/1
F1	06-07	53	10	6	2	2/0	-	7/7/9	3/1/0	1/0	2/0	-	9/6/2	1/0
F4	05-06	42	17	9	4	8/0	3/2/2	13/11/15	3/0	6/0	1/0/1	-	13/4/3	2/2/0
F4	07-08	54	15	9	3	6/0	-	12/12/15	1/0	1/0	3/0	1/1/0	10/4/2	1/0/1
F4	08-09	40	11	7	2	6/2/2	2/0	12/5/5	2/3/3	1/0	1/1/0	3/0	10/5/1	1/0/1
C6	04-05	61	10	8	1	2/0	1/0	17/8/9	-	4/0	4/1/1	4/1/0	12/5/0	1/0
C6	05-06	53	8	8	0	6/1/1	2/0	14/5/5	1/0	4/0	-	4/1/0	14/5/0	1/0
C6	07-08	54	14	10	2	1/0	-	13/9/11	1/1/1	4/0	3/2/0	-	14/4/2	-
C6	08-09	41	11	9	1	3/0	1/0	13/5/6	1/0	-	1/1/0	2/0	13/2/1	-
Total			111	77	17	36/3/3	11/2/2	109/68/81	27/12/11	24/0	19/6/3	15/3/0	114/39/12	14/4/3

Table 2.3.—Number of fetuses assigned to known-age parents in supplemented enclosures. Table illustrates number of sampled known-age candidate parents available before population adjustments and number of known-age parents during 2004 to 2009 in southern Texas. Enc. = Enclosure, N = Estimated population size derived from camera surveys, L = genotyped litters, S = singletons, T = twins, U = age unknown. Low density = <25 deer, medium density = 25 to 39 deer, high density = >40 deer.

Enc.	Year	N	L	S	T	Sires/Females/Offspring				Dams/Singletons/Twins				
Low Density						1	2	3+	U	0.5	1	2	3+	U
F2	04-05	10	2	2	0	-	-	2/0	1/0	1/0	1/1/0	1/1/0	2/0	-
F2	06-07	7	4	1	3	2/1/1	1/0	3/4/5	-	-	-	2/0/2	2/1/1	4/0
F2	07-08	12	1	0	1	-	2/1/2	-	-	-	-	1/0	3/0/1	1/0
F2	08-09	13	1	1	0	-	-	2/1/1	-	1/1/0	1/0	-	4/0	-
F1	05-06	24	13	5	4	5/0	2/0	8/4/4	11/5/6	2/1/0	7/5/1	2/1/0	16/1/3	2/0
C5	04-05	19	1	1	0	-	-	3/0	4/1/1	3/1/0	2/0	-	3/0	3/0
C5	05-06	14	4	0	4	1/0	-	2/0	3/4/5	1/0	3/0	2/0/1	3/0/2	2/0
C5	06-07	11	3	0	3	-	1/0	2/2/4	-	1/0	1/0	2/0/1	3/0/2	-
C4	08-09	19	2	2	0	3/1/1	1/0	5/1	1/0	2/2/0	1/0	2/0	7/0	1/0
Total			31	12	15	11/2/2	7/1/2	27/12/15	20/10/12	11/5/0	16/6/1	12/2/4	43/2/9	13/0
Medium Density														
F1	07-08	38	5	1	4	8/1/1	2/0	10/5/7	-	4/1/0	-	2/0/2	8/0/2	1/0
F1	09-10	30	2	1	1	2/0	3/0	2/0	1/1/1	-	3/0	2/1/1	9/0	-

Table 2.3.—(Continued).

Enc.	Year	N	L	S	T	Sires/Females/Offspring				Dams/Singletons/Twins				
						1	2	3+	U	0.5	1	2	3+	U
Medium Density (continued)														
F4	04-05	32	3	0	3	5/0	5/0	15/3/6	3/0	-	-	2/0	15/0/2	2/0/1
F4	06-07	37	1	1	0	-	-	11/1/1	2/1/1	1/1/0	2/0	2/0	11/0	2/0
C4	07-08	35	3	3	0	2/1/1	3/0	4/1/1	1/0	4/3/0	1/0	-	8/0	1/0
C4	09-10	31	2	0	2	3/1/2	3/0	5/1/2	-	2/0/1	1/0/1	1/0	9/0	1/0
C6	06-07	31	2	2	1	1/0	1/0	12/2/2	1/1/2	1/0	2/1/0	-	19/1/0	-
Total			18	8	11	21/3/4	17/0	59/13/19	8/3/4	12/5/1	9/1/1	9/1/3	79/1/4	7/0/1
High Density														
F1	04-05	78	1	0	1	2/0	2/1/2	8/0	15/0	2/0	4/0	1/0	19/0	7/0/1
F1	06-07	53	7	2	5	2/0	-	7/5/7	3/2/2	2/1/0	4/2/1	1/0/1	13/0/3	1/0
F4	05-06	42	12	8	3	8/0	3/2/3	13/5/5	3/3/3	6/0	9/7/1	-	16/1/2	2/0
F4	07-08	54	4	2	2	6/1/1	-	12/3/5	1/0	2/2/0	4/0/1	2/0/1	10/0	1/0
C6	04-05	61	1	1	0	2/0	1/0	17/1/1	-	4/0	4/0	4/0	13/1/0	1/0
C6	05-06	53	1	1	0	6/0	2/0	14/1/1	1/0	4/0	1/1/0	4/0	14/0	1/0
C6	07-08	54	2	2	0	1/0	-	13/2/2	1/0	5/1/0	4/1/0	-	14/0	-
C6	08-09	41	1	1	0	3/0	1/0	13/1/1	1/0	1/1/0	1/0	2/0	13/0	-
C6	09-10	43	3	2	1	4/0	2/0	11/2/3	-	1/1/0	1/1/0	1/0/1	14/0	-
Total			32	19	12	34/1/1	11/3/5	108/20/25	25/5/5	27/6/0	32/12/3	15/0/3	126/2/5	13/0/2

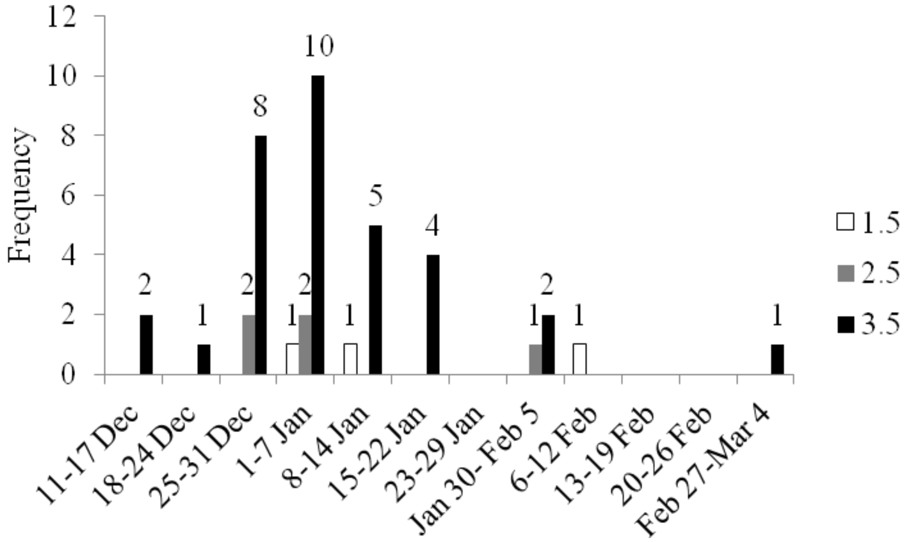

Fig. 2.1.—Temporal distribution of breeding success by male age class; data were derived from measured fetuses collected in southern Texas during 2004-2009. Data are for supplemented enclosures only; numbers above bars indicate total number of fetal litters sired by an age class.

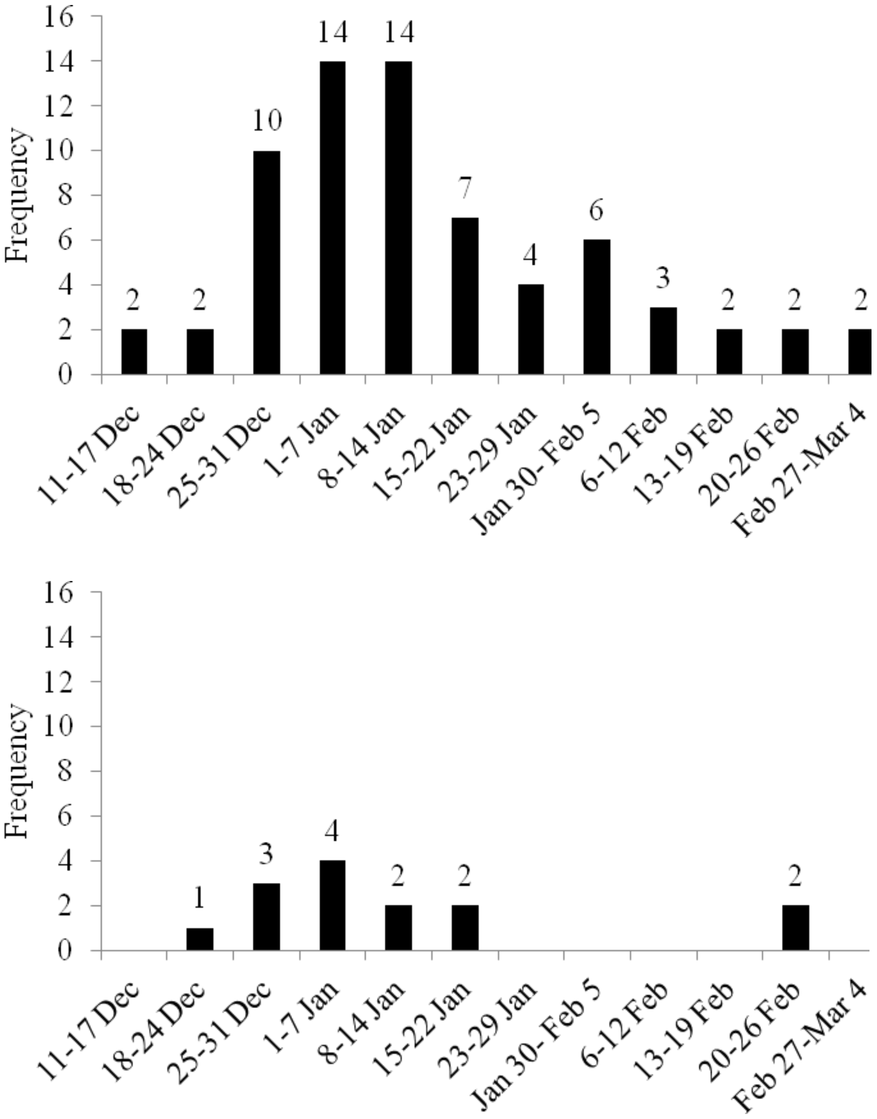

Fig. 2.2.—Distribution of conception dates for all fetal litters from supplemented (top) and not supplemented (bottom) enclosures in southern Texas during 2004-2009. Numbers represent number of fetal litters collected during study period.

Of 91 twin litters, I observed 23 (25%) cases of multiple paternity. I did not observe multiple paternity in unsupplemented enclosures, though fewer litters with >1 fetus were available (n = 11). In supplemented enclosures, 23 of 80 (29%) litters were sired by more than 1 male. I had estimated ages for ≥1 male involved for 20 litters; fourteen (70%) involved either a young male (n = 8) or a senescent male (≥7.5 year old, n = 6). I had estimated ages for both sires for 11 litters; ten of 11 involved a young male (n = 5) or senescent (n = 6) male as 1 sires. Most cases of multiple paternity included a mature male (7 of 11, 64%) as 1 of the sires, but I only observed 1 litter where both sires were prime-aged males. Overall, 39% (9 of 23) of all offspring sired by young males involved multiple paternities; most involved yearlings (7 of 12, 58%), not 2.5 year olds (2 of 11, 18%).

Reproductive success of females.—— Fawns in supplemented enclosures had higher pregnancy rates (19 of 62, 31%) than fawns in unsupplemented enclosures (1 of 8, 13%; Table 2.4, pg. 80). The remaining age classes had similar proportions. In unsupplemented enclosures, most offspring that survived to recruitment were raised by mature females (44 of 53, 83%). Only 6%, and 11% of sampled offspring were assigned to 1.5, and 2.5 year old females, respectively; doe fawns recruited no offspring. I observed a similar distribution of recruitment in supplemented enclosures. Fawns, yearlings and 2.5 year old females recruited 3%, 9% and 11% offspring, whereas mature females raised 76% (113 of 148) of offspring.

Deer density in supplemented enclosures did not appear to influence recruitment rates among female age classes. In low, medium and high density populations, 40%, 29% and 35% of young females (pooled data for 1.5 and 2.5-year old females) were

Table 2.4.—Proportion of female white-tailed deer pregnant by 4-age class in unsupplemented and supplemented enclosures in southern Texas, 2005-2009. Data were collected from females harvested during population maintenance activities during March – April.

	Female age class			
Treatment	0.5 (%)	1.5 (%)	2.5 (%)	≥3.5 (%)
Supplemented	19/62 (31)	22/25 (88)	11/11 (100)	26/28 (93)
Unsupplemented	1/8 (13)	4/5 (80)	1/1 (100)	8/8 (100)

assigned to ≥1 fawn, respectively (Table 2.3, pg. 75). In low, medium, and high density populations, 38%, 50% and 45% mature females were assigned to ≥1 fawn, respectively. Overall, supplemental nutrition had a clear effect on offspring recruited, where does in supplemented enclosures recruited almost 3 times more fawns than in unsupplemented enclosures. Proportion of available mature females that recruited offspring was 53% lower in unsupplemented enclosures (23%, 44 of 192) than supplemented enclosures (49%, 113 of 232). Differences in recruitment rates among mature females in supplemented and unsupplemented enclosures also influenced number of recruited twin fawns. In unsupplemented enclosures, only 9% (4 of 44) of mature females recruited twins compared to 31% (35 of 113) of supplemented females. Although improved nutrition during late gestation, lactation, and weaning likely influenced differences in recruitment between supplemented and not supplemented enclosures, differences in litter size may have also contributed because average number of fetuses/litter was slightly higher in mature females from supplemented enclosures (n = 26, $\bar{x}$ = 1.85, var = 0.46) than unsupplemented enclosures (n = 8, $\bar{x}$ = 1.50, var = 0.53).

I observed differences in conception dates among female age classes between unsupplemented and supplemented enclosures. In unsupplemented enclosures, 4 of 5 young females were bred during the latter portion of the breeding season, after mature females (Fig. 2.3, pg. 82). There was greater overlap in conception dates between young and mature females in supplemented enclosures (Fig. 2.3, pg. 82). Ten of 11 doe fawns conceived after the peak rut.

Assortative mating.——Of all known-age parentage assignments in supplemented enclosures, yearling males were more likely to breed with young dams (≤2.5 years old)

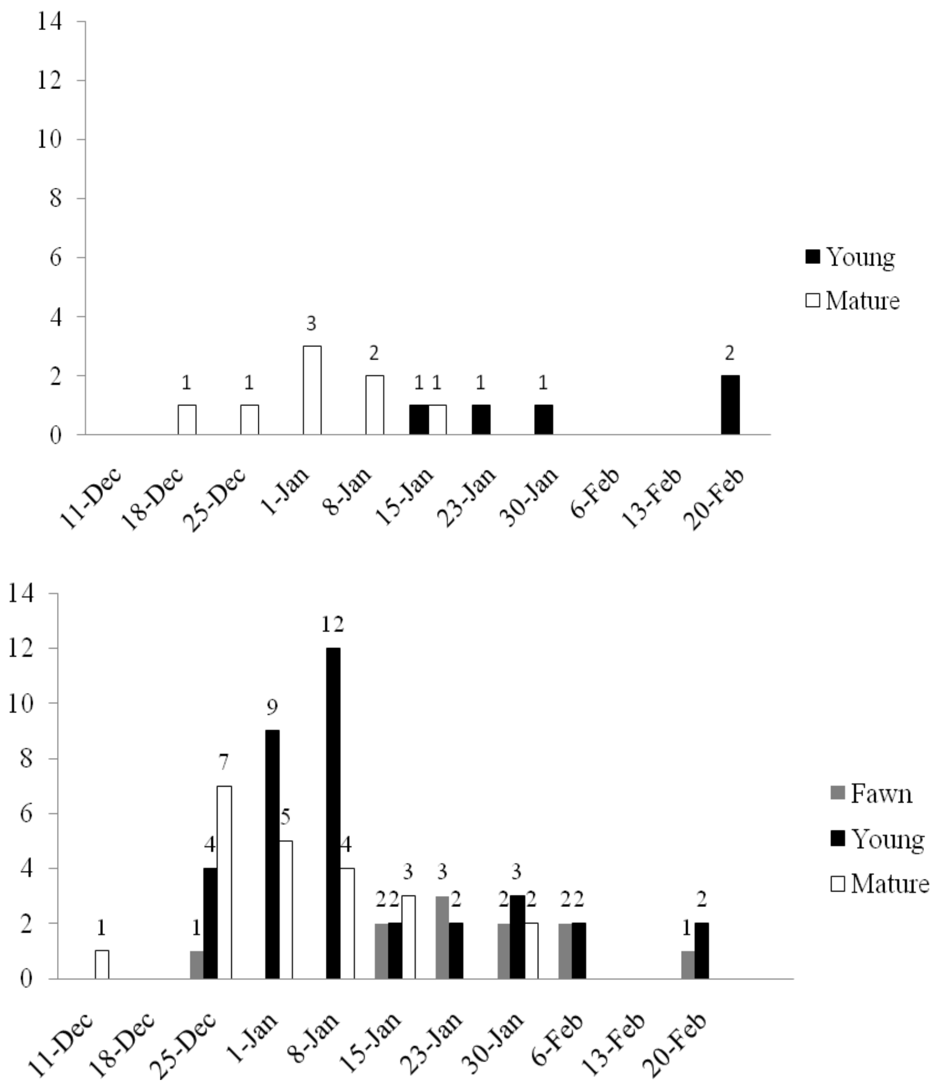

Fig. 2.3.—Estimated conception dates of fetuses from 3 female age classes (fawn, young [1-2 years old], and mature [3+ years old]) in unsupplemented enclosures (top) and supplemented enclosures (bottom) in southern Texas during 2005-2009. Values on top of bars indicate sample size for corresponding age class during a 7 day period of the breeding season.

whereas older males were more likely to sire offspring with mature (≥3.5) dams (Table 2.5, pg. 84). The tendency of young males to mate with young females did not appear to be influenced by female age structure as most populations where yearlings sired offspring were skewed towards mature females (Table 2.6, pg. 85).

Table 2.5.—Known-age parents assigned of fetuses or fawns in supplemented enclosures during 2004 to 2009 in southern Texas.

			Dam Age Class			
Sire Age Class	N sires	N offspring	0.5 (%)	1.5 (%)	2.5(%)	≥3.5 (%)
1.5	11	12	3 (25)	1 (8)	3 (25)	5 (42)
2.5	9	10	0 (0)	2 (20)	2 (20)	6 (60)
≥3.5	136	184	7 (4)	20 (11)	17 (9)	140 (76)

Table 2.6.—Number of known-age sampled females in each population when a known-age 1.5 year old male sired offspring in supplemented enclosures during 2005-2009 in southern Texas.

	Females in Population[1]					
N 1.5 year old sires	0.5	1.5	2.5	3.5+	Age of Dam	Offspring
1	4	1	0	8	0.5	Fetus
1	2	1	2	7	0.5	Fetus
1	2	1	1	9	1.5	Fetus
1	4	0	2	8	2.5	Fetus
1	0	0	2	2	2.5	Fetus
1	2	4	2	10	0.5	Fetus
1	4	0	4	14	2.5	Fawn
2	1	1	3	10	3.5+[2]	Fawn
1	0	0	2	7	3.5+	Fawn
1	1	1	0	8	3.5+	Fawn

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[1] Number of known-age females available during rut (for fetal assignment) or to recruit offspring after population maintenance periods (for fawn assignment).

[2] Both dams were 3.5+ years old.

DISCUSSION

Reproductive success of males.—— Consistent with previous studies, mature males sired most offspring and reproductive success was widespread among individuals (range 0 - 7 litters). It appears that supplemental feeders did not allow for monopolization of resources or areas. In contrast with other cervid species, white-tailed deer do not appear to be as flexible in terms of resource or harem-defense strategies.

Mature males are socially dominant over young males (Miller et al. 1987) and are physically capable of exerting greater breeding effort. Control of population densities in the supplemented enclosures required the removal of individuals. Untagged individuals were removed to maintain a known marked population; untagged deer were typically young deer (0.5 to 2.5 year olds). Unsupplemented enclosures had low reproductive rates, resulting in a mature age structure. Therefore, most populations trended to a mature age structure during the course of the study. The mature male age structure in most enclosures may have resulted in mature males siring most offspring.

Young males were most successful during peak rut when many females were in estrous at the same time. The synchronous estrus may prevent mature males from dominating access to >1 receptive female, providing opportunities for young males (e.g., DeYoung et al. 2002; Say et al. 2001). Interestingly, most cases of multiple paternity involved young males. Multiple paternities were more prevalent among yearlings (58%) than 2 year old males (18%). The discrepancy in multiple matings among age classes of males may be due to social or behavioral factors. For instance, young males may simply employ an alternative strategy, as observed in some species of ungulates (Coltman et al. 2002; Hogg and Forbes 1997). However, it is possible that mature males might not view yearling males as a rival due to the comparatively smaller antlers and body size of yearling males. Yearlings may be presented an opportunity to sneak a copulation while the tending male is occupied with confronting and chasing rivals (e.g., Isvaran 2005). Young males may encounter receptive females during peak rut, when mature males are occupied with other females. For instance, young males may employ a “sit and wait” strategy (Ch. 1), and remain in or near a female group. A sit and wait strategy may be less profitable in that fewer estrous females are encountered, but may allow access to an estrous female prior to an older male. If young males are more likely to be displaced shortly after breeding, dominant males may sire offspring in the same litter. Regardless of how young males were able to acquire mating opportunities, it is clear that intraspecific competition does not prevent young males from accessing females. In contrast, harem-defense or resource-defense strategies do not allow young males to breed if mature males are present (Mysterud et al. 2008).

Even though mature males out-numbered young males and sired most offspring, I observed an apparent nutritional influence on breeding success of young males. Young males in supplemented enclosures were able to sire offspring while unsupplemented young males did not. Therefore, access to supplemental nutrition may have allowed young males in supplemented enclosures to invest resources towards breeding activities. The finding that sampled young males (≤2.5 year old) were not responsible for any sampled offspring in unsupplemented enclosures, but were successful sires in supplemented enclosures, was unexpected. While I cannot say with certainty that young males did not sire offspring (due to unsampled individuals, poor DNA material, cast antlers, etc.), 48 young males were available as candidate sires in unsupplemented populations. Young males in unsupplemented populations may have been more limited by nutritional resources and thus were physically immature or unable to devote energy to breeding activities.

Reproductive success of females.— Females had higher reproductive rates in supplemented than unsupplemented enclosures which clearly indicate that nutrition limits reproduction in this environment. Improved nutrition may enable mature females to invest more resources in reproduction, thereby increasing fawn production. For small browsing ruminants such as white-tailed deer, forage quality limits production, especially during late gestation and lactation. In dry summers associated with south Texas, forage quality may be insufficient to support lactation. In this situation, supplemental nutrition apparently provides sufficient nutrition.

Differences in productivity of young females between supplemented and unsupplemented enclosures were striking; young supplemented females, including female fawns, appeared to be in good body condition, enabling them to enter estrous and become pregnant. The difference in overlap of conception dates between young and mature females in supplemented and unsupplemented enclosures suggest that young supplemented females are in good body condition which allows them to enter estrus earlier during the breeding season (Mitchell and Lincoln 1973; Suzuki et al. 1996).

The nutritional influence was readily apparent in mature females; these exposed to supplemental nutrition had higher recruitment rates (49% vs. 23%), fetal rates ($\bar{x}$ = 1.85 vs. 1.50), and recruited a greater proportion of multiple litters (31% vs. 9%) compared to mature females in enclosures without supplemented nutrition. However, supplemental nutrition did not translate into high rate of recruited offspring among young females. Mature females were responsible for most of the recruited offspring in unsupplemented (83%) and supplemented (76%) populations.

The supplemental nutrition increased recruitment for mature females, but not for young females. Why was the difference in recruitment between young and mature females so great? Previous studies have found access to feed may be affected by social hierarchies (Bartoskewitz et al. 2003; Donohue 2010). Mature females may have had greater access to feed than young, presumably subordinate, females. Furthermore, as density increases, access to feed or fawning cover could become limiting, as older females usually retain the most productive fawning cover (McCullough 1979). However, I did not observe a noticeable density influence on recruitment rates among young females. It is possible that enclosures did not exhibit a sufficient range of density to observe effects of social pressure on fawn-rearing. Fawn recruitment also may be dependent on maternal experience (Mech and McRoberts 1990; Ozoga 1986), though experience is usually associated with predation avoidance. It is possible that predation may have caused differences in recruitment among female age classes if experienced females may have been better able to defend or hide fawns. Coyotes are the main predator of fawns in south Texas (Ballard et al. 2001) and were actively trapped and excluded from the enclosures. However, trapping efforts may not eliminate all coyotes. Furthermore, bobcats also were present; bobcats are not considered a major predator on deer, but will predate on fawns (Ballard et al. 2001). Therefore, some combination of social interactions, maternal age and experience may have affected fawn recruitment.

Assortative mating.— Assortative mating has been suggested (e.g., Sorin 2004) but has not been demonstrated conclusively. In this study, mature males tended to copulate with mature females, whereas young males were more likely to copulate with young females which were less likely to successfully raise offspring. Because mature females were more likely to successfully recruit offspring than young females, this suggests that males may adjust their mating efforts to increase their fitness. Alternatively, females may "choose" older males (but not always, as demonstrated by mating with young females). These age-specific mating tendencies apparently influenced pre-recruitment and post-recruitment breeding success. Mature males sired 7% more recruited offspring than fetal offspring, whereas young males sired 33% fewer recruited offspring than fetal offspring. It appears that mature males have a higher probability of passing on paternal genes than young males; thus, older males may invest energy towards a resource (i.e., mature female) that is more likely to increase fitness in terms of viable offspring (Mainguy et al. 2008; Say et al. 2003). The combination of young males' increased mating success during peak rut and associative mating suggests that mature males may be concentrating on mature females within a social group.

Overall, the 2 reported instances (Sorin 2004: this study) of assortative mating occurred within enclosed populations, which may influence social interactions among males and females. More research is needed to examine assortative mating in white-tailed deer. Nevertheless, the difference in pre-parturition and post-recruitment breeding success has implications for making inferences based on parentage analysis using only fetuses or only fawns. Parentage analyses using fetuses would indicate young males sired a respectable proportion of offspring, however, such analyses using fawns would indicate lower breeding success.

It is apparent that in semi-arid environments, deer densities rarely reach carrying capacity; however, once supplemental nutrition is provided, deer densities increase which has ecological implications (Cote et al. 2004). Females of all ages appeared to have higher reproductive potential when exposed to supplemental feed however; mature females appeared to be responsible for most recruited offspring. Thus, deer management seeking herd reduction should focus on removal of mature females. Variable recruitment rates associated with nutrition and female age also have implications for male breeding effort. Lifetime reproductive success will be reduced if poor nutrition or recruitment occurs during prime years of males. My results improve understanding of the complex environmental influence on reproductive success in white-tailed deer in semi-arid rangelands.

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CHAPTER III

REPEATABILITY OF ANTLER CHARACTERISTICS IN MATURE MALE WHITE-TAILED DEER IN SOUTH TEXAS

INTRODUCTION

The nature and extent of individual variation in quantitative traits has long been a topic of interest in the ecology and management of wildlife (Nussey et al. 2007). Traits may be expressed more than once during an animal’s life, through temporal or spatial repetition of growth. In animals, temporal repetition of traits is more common, and studies of domestic animals focused on production traits such as litter size, lactation performance or wool length (Falconer and Mackay 1996). Because temporal repetition of traits varies among and within individuals, understanding the magnitude and cause of variation in trait expression is important for assessing the potential for genetic selection and how heritable traits respond to environmental variation (Hayes and Jenkins 1997).

Antlers are a sexually selected trait unique to most cervids, and are cast and re-grown each year. Antlers may serve as honest advertisements of individual condition or quality (Ditchkoff et al. 2001) and fit the definition of a handicap trait (Zahavi 1975). Antler size and overall conformation are partially genetically determined (Goss 1983, Lukefahr and Jacobson 1998), but phenotypic expression is influenced by animal age and environmental factors. For instance, antler development may be affected by maternal effects (Monteith et al. 2009) or birth date, where late-born individuals may be phenotypically stunted (Gray et al. 2002). Population density (Couturier et al. 2010; McCullough 1997) and nutrition or habitat quality (Bowyer et al. 2002; Strickland and Demarais 2000) also influence antler development through temporary and permanent effects on expression. Temporary effects on antler expression may be caused by resource limitation (Clutton-Brock et al. 1982; Geist 1986; Simard et al. 2008) such that when nutritional availability increases, improved antler growth occurs (Ashley et al. 1998; Leberg and Smith 1993). Permanent environmental effects may occur when nutritional conditions during year of birth influence general development of young males (Kirkpatrick and Lande 1989; Mech et al. 1991), which may have long lasting effects on antler traits throughout life (Monteith et al. 2009). Finally, population density and resource limitation may modify life history to adjust body mass and reproduction (Gaillard 1998; Simard et al. 2008). As a result, it is difficult to separate the effects of environmental and genetic components of variation on the expression of antler traits.

The effects of environment on antler growth have been assessed mainly in northern populations of cervids (Mysterud et al. 2005; Schmidt et al. 2001). Variable precipitation in arid environments influences population dynamics of ungulates (Marshal et al. 2002; Owen-Smith 1990) but the influence of climate on antler growth in semi-arid environments has not been quantified. Southern Texas and northern Mexico experience dramatic year-to-year variation in rainfall (coefficient of variation >30%). The 60 years preceding the year 2006 produced 23 wet summers and 37 dry summers; total rainfall ranged from 40 to 120 cm (Norwine and John 2007). This semi-arid environment provides opportunities to quantify how environmental variability affects individual variation in a sexually selected quantitative trait. The source and magnitude of variation in antler expression, as an individual characteristic, under different environmental conditions has implications for honest advertisement of condition or quality (Zahavi 1975). Furthermore, antlers are both targets and tools in the management of cervid populations (Demarais and Strickland 2011; Miller and Marchinton 1995). Understanding the magnitude of environmental effects on antler traits has practical applications for the consideration of antler characteristics in harvest decisions (Demarais and Strickland 2011; Miller and Marchinton 1995; Mysterud and Bischof 2010).

I assessed the role of environmental effects on antler growth using a quantitative genetic model involving a temporally extensive dataset of free-ranging white-tailed deer (*Odocoileus virginianus*). I estimated repeatability, the correlation between repeated measurements on a quantitative trait separated by space or time. Repeatability is defined as ratio of among-individual variance to total variance of a measured trait, which also sets the upper limit of heritability (Falconer and Mackay 1996). My objectives were to derive repeatability estimates for antler traits in wild populations and to determine how variable rainfall and enhanced nutrition affect repeatability of antler traits.

STUDY SITES

I used 7 study sites in South Texas; 1 in Kleberg County, 4 in Webb County, and 2 in Dimmit County (Fig. 3.1, pg. 102). The Kleberg site was located 16 km east of Kingsville, Texas and was part of the Southern Subhumid Gulf Coastal Prairie ecoregion (EPA 2010). Typical woody plants included huisache (*Acacia farnesiana*) and mesquite (*Prosopis glandulosa*). The 4 sites in Webb County (Webb1 to Webb4) were located 43 km east, 29 km east, 15 km northeast and 24 km northeast of Laredo, Texas, respectively and were part of Texas-Tamaulipan Thornscrub ecoregion (EPA 2010). Typical woody vegetation included mesquite, brasil (*Condalia hookeri*), and lime pricklyash (*Zanthoxylum fagara*). Dimmit county sites 1 and 2 were 48 km southwest and 23 km northwest of Carrizo Springs, respectively and were part of the Texas-Tamaulipan

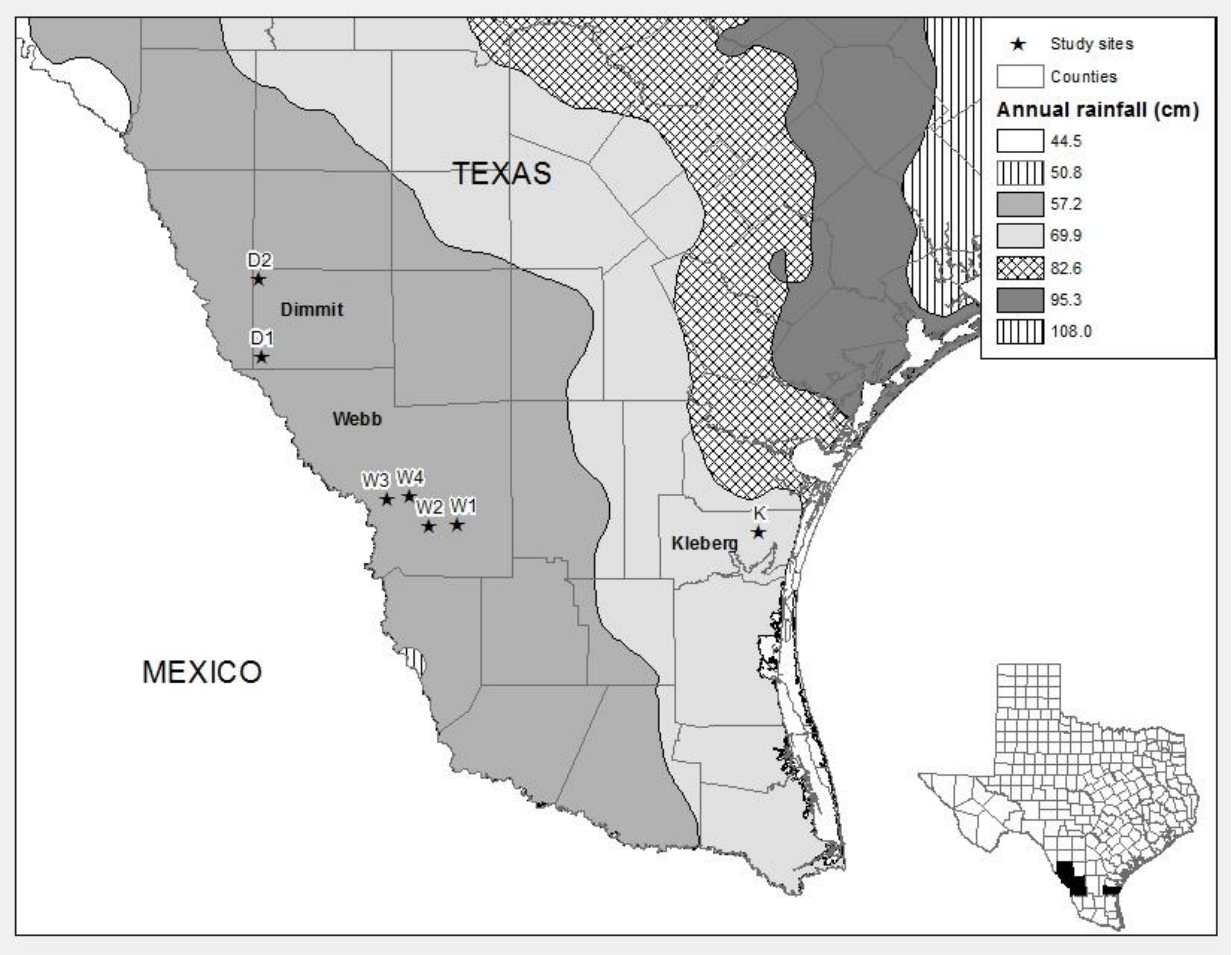

Fig. 3.1.—Locations of 7 study sites in South Texas and average rainfall isohyets for the region.

Thornscrub ecoregion (EPA 2010).

METHODS

Deer capture and antler measurements.—— I captured deer using the helicopter net-gun (Barrett et al. 1982, Webb et al. 2008) or drive-net techniques (DeYoung 1988) I captured 30 to 150 male deer annually from each site for 4 to 10 years, depending on the site. Helicopter pilots were instructed to capture the first antlered deer encountered. I estimated age according to tooth replacement and wear (Severinghaus 1949). I either inserted unique numbered microchips (Avid Microchip ID Systems, Mandeville, LA, USA) subcutaneously in the front leg and at the base of one ear or attached unique numbered and colored livestock ear tags to both ears. I released deer near capture locations. Hunting occurred on some of the sites during the study period and served as additional means for re-sampling previously captured individuals. Deer captures were approved by Texas A&M University-Kingsville Institutional Animal Care and Use Committee (Animal Use Protocol numbers 3-98-09, 99-5-2, 2003-5-14, 2009-05-6A) and were consistent with guidelines approved by the American Society of Mammalogists (Gannon and Sikes 2007).

I measured length and circumference of antlers using the Boone and Crockett system (B&C; Nesbitt and Wright 1981). Antler size was the sum of 4 circumferences of main beams, lengths of main beams, lengths of antler points (if ≥2.54 cm), and the greatest spread between the main beams. Measurements were taken using a metal tape to the nearest 0.317 cm. Total number of antler points was the count of points ≥2.54 cm in length. The sole exception to my antler measurement protocol was site Dimmit1, where only 1 basal circumference of both main beams was recorded to minimize processing time during capture (see below for analysis).

Repeatability.—— Repeatability is the sum of additive and non-additive genetic variation and permanent environmental variation divided by total variation (Falconer and Mackay 1996). Additive genetic variation, the basis of heritability, is the sum of the independent effects of individual genes' influence on an expressed trait of an individual (Falconer and Mackay 1986). Permanent environmental effects potentially include non-additive genetic effects, maternal condition, range conditions (e.g., birth year), or physical injuries that have permanent consequences on the individual (e.g., Gaillard 1993). Residual variation includes temporary environmental effects, such as drought effects on antler traits in one year. Temporary environmental effects also may include foraging ability, health status, and social status (Lukefahr and Jacobson 1998).

I estimated repeatability of antler traits using an animal model (Henderson 1953). All analyses were done using the computer program LSMLMW (least squares maximum likelihood mean weighted; Harvey 1987), and I used capture year as my fixed effect and animal as my random effect. Variation of a measured trait is separated into 2 categories: repeatability and residual variation, which always sum to 1. Repeatability values range from 0 to 1; values of 0 indicate that the average of repeated antler measurements from all individual males is identical and variation is entirely within individuals. Values of 1 indicate the same antler measurements are obtained every time an individual is captured and all variation is among individuals (Hayes and Jenkins 1997). For simplicity, I classified repeatability values <0.30 as low, 0.30-0.60 as moderate, and >0.60 as high.

Males typically develop small antlers as yearlings and continue to increase in antler size until about 5 years of age (after attaining physical maturity) then may not change dramatically until senescence at >7 years old (Lewis 2010). Antler size thereafter usually decreases. Due to the change in antler size from 1 to 3 years old, I used measurements only from prime-age males (aged 3 to 6 years old) on 6 of 7 sites. Data collected from Dimmit1 were previously reported in DeYoung (1998) and included males aged >6 years old. Inaccuracies of the tooth wear and replacement method (Gee et al. 2002; Lewis 2010) complicate the assignment of specific year classes due to variation among individuals within age classes. However, white-tailed deer in South Texas can be assigned to age classes 2.5 years, 3.5 to 5.5 years and >6.5 years of age with acceptable accuracy (72%, 73%, and 68%, respectively; Lewis 2010).

Most individuals were captured before the breeding season and broken antlers were rare (Webb et al. 2008). Antler points or main beams broken prior to or during capture were removed from specific analyses. For instance, an individual with a broken main beam was removed from analyses incorporating main beam measurements but was considered for analyses of individual traits not affected by the broken portions, such as inside spread or number of antler points. Broken antler points ≥2.54 cm were included in analyses of total number of antler points, but not in analyses requiring length of antler points. To minimize data removal due to broken antlers and asymmetry between a set of antlers from an individual, I treated left and right antlers separately (measurements from left and right antlers were not combined). The spread between main beams is not a measurement of antler size or mass. Therefore, I subtracted the inside spread measurement from the B&C score and termed the modified score as “total antler length”.

Because site Dimmit1, an unfed site, did not record all measurements, I compared the correlation among different combinations of antler trait measurements from the Kleberg population, another unfed site. Sum of antler point length in Dimmit1 had the highest correlation with total antler length ($r^2 = 0.84$) in Kleberg thus, I used sum of antler point length in lieu of total antler length for Dimmit1. Repeatability values for traits with multiple measurements (basal circumference and main beam length) were averaged for each site.

Rainfall and enhanced nutrition.—— I used a quasi-experimental approach (Morrison et al. 2008) to assess the effects of environmental variation on repeatability of antler traits. My treatments were not randomly assigned to study sites, thus, my experiment was not designed with equal numbers of controls and treatments. Furthermore, sites were exposed to uncontrolled environmental conditions for the duration of capture. Antler growth in male white-tailed deer begins during spring and ceases in early autumn (Sauer 1984). Consequently, rainfall during March to May is important because of its impact on forage production and quality during the antler growing period. Total rainfall in March to May during years of capture on each site averaged 15.2 cm ($\sigma^2 = 39.9$), 9.6 cm ($\sigma^2 = 11.8$), 9.6 cm ($\sigma^2 = 11.8$), 9.6 cm ($\sigma^2 = 11.8$) and 9.2 cm ($\sigma^2 = 14.9$), 14.6 cm ($\sigma^2 = 51.2$), and 18.1 cm ($\sigma^2 = 60.3$) for sites Kleberg, Webb1, Webb2, Webb3, Webb4, Dimmit1, and Dimmit2, respectively (www.met.tamu.edu/osc/tx/; http://www7.ncdc.noaa.gov/IPS/coop/coop.html). I first grouped sites based on relative rainfall variance during the 4 to 10 years of data collection; sites Kleberg, Dimmit1, and Dimmit2 were categorized as variable rainfall (σ^2

≥ 39.9 cm) and sites Webb1, Webb2, Webb3, and Webb4 were categorized as consistent rainfall ($\sigma^2 \leq 14.9$ cm).

Many private land owners in South Texas provide enhanced nutrition as part of their deer management programs (Jacobson et al. 2011; McBryde 1995). Intensity of feeding varied among the study sites; some sites had a greater density of feed stations or provided feed year-round versus during a portion of the year. I categorized sites into quasi-treatment groups based on feed intensity (unfed, moderate, and intensive). Kleberg and Dimmit1 did not provide enhanced nutrition and served as unfed controls. Webb1, Webb2, and Dimmit2 had intensive feed programs, defined as constant feeding year-round. Webb3 and Webb4 had moderate intensity feed programs, defined as not feeding year-round. Enhanced nutrition programs consisted of commercial pelleted rations provided *ad libitum*. Pellets contained ≥16% crude protein, ≤12% fiber, ≥2% fat and contained minerals (calcium, phosphorus, salt, etc.) and vitamins (A and E).

I used 95% confidence intervals to evaluate differences in mean repeatability of same antler traits among feed (n = 3) and rainfall (n = 2) quasi-treatments.

RESULTS

I captured 233 to 856 unique individuals per site and 98 to 235 individuals per site were recaptured ≥1 times. Number of records removed from analysis because of broken antlers was low, ranging from 0 to 6 occurrences per site for each trait. Number of antler points had lowest average repeatability ($\bar{x} = 0.55$, $\sigma = 0.09$) relative to other traits, regardless of site. Inside spread ($\bar{x} = 0.69$, $\sigma = 0.07$) and beam length ($\bar{x} = 0.66$, $\sigma = 0.05$) had the highest average repeatability. Total antler score and basal circumference were moderately repeatable (0.59-0.60, 0.54-0.58, respectively) in 2 of 7 sites and highly repeatable (0.64-0.82, 0.65-0.70, respectively) in 5 of 7 sites. Number of antler points was moderately repeatable (0.42-0.59) in 5 of 7 sites and highly repeatable (0.61-0.64) in 2 of 7 sites. Main beam length was highly repeatable (0.60-0.74) in all sites. Inside antler spread was highly repeatable (0.66-0.80) in 6 of 7 sites and moderately repeatable (0.58) in the remaining site (Table 3.1, pg. 109).

Total antler score repeatability was 16% lower in variable rainfall sites ($\bar{x}$ = 0.62, σ = 0.05, 95% CI = 0.57-0.68) than more consistent rainfall sites ($\bar{x}$ = 0.74, σ = 0.09, 95% CI = 0.65-0.83). Repeatability of number of antler points appeared to be affected by rainfall regardless of enhanced nutrition availability (Table 3.1, pg. 109). Repeatability of number of antler points was 24% lower in sites with variable rainfall ($\bar{x}$ = 0.45, σ = 0.03, 95% CI = 0.41-0.48) versus consistent rainfall ($\bar{x}$ = 0.59, σ = 0.06, 95% CI = 0.53-0.64).

Unfed sites had lower total antler score repeatability ($\bar{x}$ = 0.60, σ = 0.01, 95% CI = 0.59-0.60) than sites with high feed intensity ($\bar{x}$ = 0.66, σ = 0.02, 95% CI = 0.64-0.69) and with moderate feed intensity ($\bar{x}$ = 0.82, σ = 0.01, 95% CI = 0.81-0.82, Table 3.1, pg. 109). Enhanced nutrition availability in variable rainfall sites appeared to moderate environmental effects from some antler traits. Repeatability estimates for total antler score and basal circumference in variable rainfall sites were 13% and 18% higher when feed was available, respectively. Sites with moderate feed intensity and consistent rainfall had 24% higher total antler score repeatability estimates ($\bar{x}$ = 0.82) than sites with high feed intensity and consistent rainfall ($\bar{x}$ = 0.66, σ = 0.04, 95% CI = 0.62-0.69; Table 3.1, pg. 109).

Table 3.1.—Capture years, number of animal records, average antler size (SE), enhanced nutrition intensity (int = intense, mod = moderate), rainfall variation (var = variable, con = consistent), and average repeatability (SE) for prime aged males from 7 South Texas sites and Mississippi State University. TAL = total antler length, BC = basal circumference.

Site	Years	N	$\bar{x}$ TAL	Feed	Rain	TAL	Points	Beam	Spread	BC
Kleberg	1999-2009	321	278.3 (50.0)	None	Var	0.59 (0.07)	0.42 (0.09)	0.68 (0.08)	0.58 (0.07)	0.54 (0.07)
Dimmit1	1985-1997	648	N/A[1]	None	Var	0.60	0.48	0.60	0.71	0.58
Dimmit2	2007-2009	186	249.3 (45.4)	Int	Var	0.68 (0.07)	0.44 (0.11)	0.64 (0.08)	0.66 (0.07)	0.66 (0.07)
Webb1	1998-2007	633	255.5 (48.7)	Int	Con	0.64 (0.05)	0.61 (0.05)	0.62 (0.05)	0.66 (0.05)	0.66 (0.05)
Webb2	1998-2008	737	259.5 (51.6)	Int	Con	0.68 (0.04)	0.59 (0.05)	0.70 (0.04)	0.67 (0.04)	0.70 (0.04)
Webb3	1998-2007	313	236.2 (46.7)	Mod	Con	0.81 (0.04)	0.51 (0.10)	0.61 (0.08)	0.72 (0.06)	0.65 (0.07)
Webb4	1998-2005	307	260.8 (50.1)	Mod	Con	0.82 (0.03)	0.64 (0.06)	0.74 (0.05)	0.80 (0.04)	0.69 (0.05)
Captive [2]	1977-1993	469	N/A	N/A	N/A	N/A	0.48 (0.14)	0.58 (0.15)	0.60 (0.12)	0.57 (0.14)
Captive [2]	1977-1993	469	N/A	N/A	N/A	N/A	0.39 (0.14)[3]	0.14 (0.15)[3]	0.03 (0.11)[3]	0.29 (0.14)[3]
Captive [2]	1977-1993	469	N/A	N/A	N/A	N/A	0.09 (0.13)[4]	0.44 (0.15)[4]	0.57 (0.12)[4]	0.28 (0.13)[4]

[1] Not all antler measurements were recorded

[2] from Lukefahr and Jacobson 1998

[3] Heritability (additive genetic effects)

[4] Permanent environmental effects

DISCUSSION

Previous studies have monitored individual populations over time to determine the effects of nutrition, body condition, and age on antler expression. My study is unique in evaluating a temporally and spatially extensive data from multiple free-ranging populations with a quasi-manipulative component in enhanced nutrition and rainfall. Observed repeatability estimates were similar to those previously reported for antler traits in white-tailed deer (Table 3.1, pg. 109) and other cervids (Table 3.2, pg. 111). Overall, captive and supplemented populations consistently have higher repeatability for antler traits than not supplemented free-ranging populations. Captive conditions provide food, shelter, protection from predators, and veterinary treatment which may reduce environmental variation due to temporary effects in antler expression. In this study, sites exposed to variable rainfall had lower repeatability than sites with consistent rainfall. However, enhanced nutrition appeared to reduce the environmental effects of rainfall variation. Sites with feed had higher average repeatability estimates than sites without feed, irrespective of rainfall. Of 3 sites exposed to variable rainfall, the site with enhanced nutrition had 15% higher total antler score repeatability.

In semiarid regions, variable rainfall affects forage quality and quantity. Forage quality is important for a concentrate selector such as the white-tailed deer, because the digestive system does not afford the opportunity to offset low-quality diets by increasing forage intake (Barboza et al. 2009). Male deer that consume supplemental feed may exhibit greater body mass and antler size than individuals without access to feed (Bartoskewitz et al. 2003). However, the highest observed repeatability values occurred at moderately fed sites, rather than intensively fed sites. A decline in repeatability might

Table 3.2.—Repeatability estimates (SE) of antler mass (g) and total antler length for populations of cervids maintained under different environmental conditions.

Species	Habitat Description	Repeatability	Authors
Red Deer[1]	Free ranging, unfed, temperate	0.57	Kruuk et al., 2007
Kleberg[2]	Free ranging, unfed, semi-arid	0.59	This study
Dimmit1[2]	Free ranging, unfed, semi-arid	0.60	This study
Red Deer[1,3]	Captive, pasture, some feed	0.64	V.d. Berg and Garrick, 1997
Webb1[2]	Free-ranging, fed, semi-arid	0.64	This study
Dimmit2[2]	Free-ranging, fed, semi-arid	0.67	This study
Webb2[2]	Free-ranging, fed, semi-arid	0.68	This study
Red Deer[1]	Captive, pens, fed	0.75	Bartos et al., 2007
WTD[1]	Captive, pens, fed	0.76	Lukefahr and Jacobson, 1998
Webb3[2]	Free ranging, some feed, semi-arid	0.81	This study
Webb4[2]	Free ranging, some feed, semi-arid	0.82	This study

[1] = mass (g)
[2] = total antler length
[3] = in velvet

also occur if antler size increased later in life as a function of enhanced nutrition. However, I detected no difference in average antler size among sites nor in ages of peak antler size between the 2 feed treatments. Average antler size peaked at 5.5 years of age in both treatments. Competition at feed sites might result in biased access to feed among individuals (Bartoskewitz et al. 2003; Donohue 2010). However, standard deviation of total antler score did not appear to covary with feed intensity. Increased feed intensity may have other demographic effects such as increased deer density, which may ultimately influence forage availability. Alternatively, inherent differences in soil or habitat quality may have impacted the results. Nonetheless, it appears enhanced nutrition reduces some of the environmental effects on antler expression.

The similar repeatability values for populations maintained under like conditions suggests that non-genetic factors affect antler expression in species of cervids in a similar manner. The influence of environmental factors on the expression of antlers is consistent with theoretical expectations for sexually selected traits. The handicap principle states that if antlers function as an honest advertisement of individual condition or quality, the trait must be costly to produce or maintain (Zahavi 1975). Individuals in good condition can afford to devote additional resources towards antler expression, but cannot maintain the investment in times of poor nutrition. In this manner, cheating strategies are curtailed in part by risking over-allocation of scarce resources to a deciduous trait in poor years. Furthermore, the use of antlers in fighting further limits cheating in that antlers must maintain a minimum threshold of strength or risk breakage, hampering the ability to compete with conspecifics during the breeding season. However, an alternative strategy to an overall reduction in antler size might be to alter antler conformation.

Number of antler points had the lowest repeatability relative to other antler traits, which suggests a potential trade-off in antler trait investment. Visual appearance is a factor in judging rivals prior to broadside threats (Clutton-Brock 1982; Lincoln 1972), yet the visual appearance of individual white-tailed deer with similar antler height, spread and beam length may be nearly identical within a range of antler points (i.e., 8-10 points). Branched antlers are used as leverage during pushing and shoving when battling with other males (Goss 1995), which suggests antler strength (i.e., mass), not necessarily the number of antler points, would be advantageous. The lower repeatability of antler points relative to traits that define overall visual appearance and strength (mass, beam length, total antler length) suggests that males may sacrifice number of antler points when nutrition is limited to maintain overall size and breaking strength.

Repeatability estimates also have implications for hunter selection and harvest management. Many state agencies have established county or state-wide harvest criteria based on antler traits, usually aimed at protecting young males from harvest (Demarais and Strickland 2011). Elsewhere, antler traits are considered in harvest decisions, where sportsmen may preferentially harvest the largest antlered males, or where antler traits are used in culling decision (Jacobson et al. 2011; Mysterud and Bischoff 2010). Commonly used criteria are number of points and antler spread due to ease of visual confirmation hunters. Number of antler points had the lowest repeatability values in this study and in previous studies (Bartos et al. 2007; Lukefahr and Jacobson 1998) whereas spread and main beam length had the highest average repeatability values. Ultimately, the choice of harvest criteria depends on whether the management objectives involve protecting young males or allowing the harvest of males with above- or below-average antler traits.

Regardless, the potential for hunter selection to affect trait evolution has raised concern (Coltman et al. 2003; Darimont et al. 2009; Harris et al. 2002; Mysterud and Bischof 2010).

Traits with heritability values above 0 have existent additive genetic variance to respond to selection (Hayes and Jenkins 1997). Heritability varies widely among age classes and among antler traits (Lukefahr and Jacobson 1998). My results suggest that traits with moderate to high heritability (h^2) appeared to be more sensitive to environmental conditions than traits with low heritability ($h^2 = <0.20$). Number of points ($h^2 = 0.39$), basal circumference ($h^2 = 0.29$), and total antler score ($h^2 = 0.43$; Lukefahr and Jacobson 1998) in variable rainfall sites had lower repeatability (31%, 15%, and 21% lower, respectively) than in sites with consistent rainfall. The aforementioned traits were 24%, 17% and 19% lower in unfed sites than fed sites. Antler spread ($h^2 = 0.03$) was 8% and 5% lower in variable rainfall sites and unfed sites than consistent rainfall sites and fed sites, respectively. Main beam length ($h^2 = 0.14$) was 3% and 5% lower in variable rainfall sites and unfed sites than consistent rainfall sites and fed sites, respectively. If heritability of antler traits in wild deer is similar to captive deer, harvest criteria based on traits that have high repeatability but low heritability might avoid negative trait evolution. Similarly, the potential for trait evolution via selection appears lower in variable environments because individuals may have good potential but poor current year growth, as observed by Kruuk et al. (2007).

Environmental effects on antler expression are pervasive in the aggregate, but the effects of specific stressors are difficult to quantify. For instance, 60 to 70% of variation in antler yield of farm-reared cervids was due to non-additive and environmental effects, even under controlled conditions (Wang et al. 1999). Similarly, I detected variation in antler expression, but could not quantify the specific causal factors involved. For instance, white-tailed deer are continuously distributed in South Texas, but I observed relatively large differences in repeatability among populations in close proximity (e.g., Webb County). Therefore, variation in repeatability may be partly due to factors such as soil or habitat quality, or management actions (Strickland and Demarais 2008). Additional research is needed to understand the nature of the environmental influence on antler expression, especially the role of maternal and cohort effects.

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