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MOVEMENTS, RELATEDNESS AND MODELED GENETIC
MANIPULATION OF WHITE-TAILED DEER

By

Stephen Lance Webb

A Dissertation
Submitted to the Faculty of
Mississippi State University
in Partial Fulfillment of the Requirements
for the Degree of Doctor of Philosophy
in Forest Resources
in the Department of Wildlife and Fisheries

Mississippi State, Mississippi

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MOVEMENTS, RELATEDNESS AND MODELED GENETIC
MANIPULATION OF WHITE-TAILED DEER

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White-tailed deer (*Odocoileus virginianus*) have been intensively studied across their range. However, many aspects of the white-tailed deer's ecology have not been studied or are difficult to study. The advent of global positioning system (GPS) collar technology and molecular genetics techniques now allows researchers to collect fine-scale and cryptic phenomena. In addition, selective harvest of male white-tailed deer, based on antler size, has not been critically evaluated. Thus, development and use of quantitative genetics models will be useful for elucidating the effects of selective harvest on mean population antler size.

I used GPS collar technology to further understand white-tailed deer movement ecology. First, I determined the efficacy and influence of a high-tensile electric fence (HTEF) on deer movements. The HTEF controlled deer movements when properly maintained and had little influence on deer spatial dynamics, making it a safe and cost-effective alternative to traditional fencing. Second, I studied fine-scale deer movements

using GPS collars collecting locations every 15 minutes. Hourly deer movements were greatest in the morning and evening. Parturition and rut influenced movements of females and males, respectively whereas weather and moon phase had minimal influence on movements.

Molecular genetics techniques are becoming more widespread and accessible, which may allow insight into the link between genetics and antler size. I found deer in 3 diverse populations from Mississippi, Oklahoma and Texas were relatively heterozygous and unrelated. Groups of deer with similar antler characteristics did not appear to be inbred or share common ancestors. In addition, there was not a strong link between individual multi-locus heterozygosity and antler points or score.

Selective harvest has been implicated in causing negative evolutionary and biological responses in several ungulate species. To better determine how selective harvest (i.e., culling; the removal of deer with inferior antlers) affects white-tailed deer antler size, I used quantitative genetic models to simulate response of deer antlers to selection. In simulated controlled breeding situations response to selection was rapid, resulting in improvement in antler size. In simulated free-ranging populations response of antler size to selection was slow and only resulted in minimal increases in antler points after 20 years.

Key words: antlers, electric fence, genetics, heterozygosity, home range, inbreeding, models, movements, *Odocoileus virginianus*, selective harvest, weather, white-tailed deer

DEDICATION

This dissertation is dedicated to my entire family; my wife Krisan, parents Del and Patricia, and sister Christy, because everyone deserves credit for whom and where I am today. Thanks for your motivation, love and support.

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CHAPTER I

INTRODUCTION

Movements within and across population boundaries are influenced by numerous ecological variables and have potentially significant effects on success of management schemes. The white-tailed deer (*Odocoileus virginianus*) is one of the most widely studied wildlife species in North America. However, many aspects of white-tailed deer ecology have not been studied at very fine temporal scales of <1 hour. The advent of global positioning system (GPS) collar technology now allows researchers to collect very accurate, fine-scale temporal data at levels not previously obtainable. Molecular genetic studies are also becoming more widespread due to the advent of new molecular genetics techniques, which may allow insight into the effects of relatedness or inbreeding on observed antler traits. Although white-tailed deer have been widely studied, many ecological and genetic aspects of deer management, including selective harvest plans, have not been critically evaluated.

Understanding deer movement, including daily movements within the home range, is an important prerequisite to understanding the species' behavior, ecology, and management (Sanderson 1966). Drawing inferences about effects of environmental conditions on deer movements requires comparisons between environmental variables and deer behavior over many years (White and Garrott 1990) or very intensively.

Intensive sampling is required when attempting to correlate short-term phenomena (White and Garrott 1990) to movements or activity. The popular literature is full of information on the effects of weather and moon phase on white-tailed deer activity, but few scientific studies have been conducted on movement patterns. Environmental effects on deer also may be confounded when deer are confined by impermeable fences (i.e., 2.5-m high fences) because deer may have altered movement patterns.

When a high fence is constructed, a deer's home range or movements may be affected. The smaller the area under high fence the greater the chances deer behavioral patterns, disease transmission, genetics, and habitat will be affected. However, deer should be able to adapt rather quickly if basic habitat requirements are met within the enclosure (Demarais et al. 2002). For these reasons, I studied the effects of an electrified high fence and environmental conditions on deer spatial dynamics. Specifically, my objectives were to: 1) determine the efficacy of a high-tensile electric fence to control white-tailed deer movements and evaluate its influence on deer spatial dynamics, and 2) determine how demographic and environmental variables affect fine-scale deer movements.

Selective harvest of males intends to reduce the number of males with lower than average antler size by selecting them for harvest prior to the breeding season. Although a variety of selective harvest approaches have been designed for white-tailed deer (e.g. antler point restrictions, minimum spread, and score), potential genetic effects have not been evaluated (Thelen 1991). Many years of data are needed to determine the effects of selective harvest plans on population antler characteristics. Effectiveness of selective

harvest may be confounded by other management practices (e.g. habitat improvement, population reduction) making response due to selection difficult to measure. Modeling the effects of harvest plans can help managers evaluate the potential positive or negative effects on population antler size as well as amount of effort required. I used a simulation model to address the effects of selective harvest plans on population antler size with varying demographic parameters. My objective was to model how variations in population demographics and heritability affect the response of white-tailed deer antlers to selection.

Reliable estimates of heritability (defined as the total variation of a phenotype, or metric trait, that is attributable to the average effects of genes) are needed when formulating selective harvest strategies, in predicting rate of genetic progress, and for recommending harvest management programs (Lukefahr 1997). Antlers are a quantitative trait expressed in males. However, the identity and number of genes, as well as potential interactions among genes (e.g. epistasis, dominance, etc.), are unknown. Antler traits are heritable (Williams et al. 1994, Lukefahr and Jacobson 1998, Kruuk et al. 2002), so male offspring should resemble fathers and close relatives should bear some similarity to one another. Most individuals share the basic antler configuration of 2 main beams and antler tines projecting upwards from the main beam. Other factors such as injury, illness, and environmental conditions can exert a strong influence on phenotype. The degree to which individuals in a population with similar phenotypes are related is unknown. I evaluated the potential influence of genetics (i.e., inbreeding and relatedness) on phenotypic expression of antler characteristics using 3 managed populations of white-

tailed deer. My objective was to estimate the association between male deer relatedness and inbreeding, as measured by homozygosity, with the expression of antler characteristics. These data will provide useful information for a wide range of management practices, which relate to high-fencing, movements, genetics, selective harvest, and antler size.

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CHAPTER II
EFFICACY OF A 15-STRAND HIGH-TENSILE ELECTRIC FENCE
TO CONTROL WHITE-TAILED DEER MOVEMENTS

ABSTRACT

Although high-tensile electric fences (HTEF) have gained in popularity as a low-cost alternative to traditional fence designs, little research has focused on the effects of HTEF on white-tailed deer (*Odocoileus virginianus*). My objectives were to: determine the efficacy of a HTEF to control deer movements and evaluate its influence on deer spatial dynamics. I conducted this study on the Samuel Roberts Noble Foundation Wildlife Unit located in Oklahoma, USA. An electric 15-strand, 2.5 m high fence was erected around the study area in 1992. I captured and ear-tagged 419 deer from 1993-2005 and fitted 35 of these deer (19 females, 16 males) with GPS collars during winter 1998-2004. Eight of 35 radio-collared deer (23%) crossed through the fence a total of 15 times and returned 13 times. Most fence crossings were at or near a hole or water gap (75%; $n = 21$) while 21.4% ($n = 6$) crossed through the electrified strands. Twenty four of 419 (6%) ear-tagged deer were reported dead or harvested off of the property over 13 years. I found ≥ 13 deer core areas and ≥ 29 of home ranges bordered the fence. Core area and home range sizes of males and females were larger for deer associated with the fence compared to deer not associated with the fence. The percentage of deer fixed

kernel core area and home range perimeters in common with the fence was 17 and 28%, respectively. It appears deer were tolerable of the fence and willing to attempt to cross at weak locations (i.e., holes and water gaps). If fully maintained, the 15-strand HTEF would have been a safe and effective alternative to more traditional and expensive fence designs.

INTRODUCTION

Fences have a wide range of uses and the type and configuration chosen is dependent on the purpose. Historically, fences were primarily erected to control damage of crops and plantings by wild ungulates (Fitzwater 1972). More recently, fences have been constructed to restrict ungulate movements and confine exotic wildlife (Demarais et al. 2002), limit public access (Brothers and Ray 1998), reduce animal damage to vehicles and plantings (Conover 2002), and restrict animal movements in urban areas (Bryant et al. 1993).

High-tensile electric fences (HTEF) have gained popularity in some western states (Karhu and Anderson 2006) due to the high-tensile strength of the strands (i.e., 11,952-14,061 kg force/cm²; McCutchan 1980), relative effectiveness of controlling movements, resistance to damage by big game and livestock, and less cost compared to traditional fence types (Byrne 1989). Deer should try to pass through the 15-strand HTEF rather than jumping over the 2.5 m high fence, which should expose them to a high voltage shock and deter them from additional attempts (Byrne 1989). Thus, HTEF should provide both a physical and psychological barrier to deer (VerCauteren et al. 2006).

The success of a fence at controlling animal movements will depend on design, wildlife species, and the motivation of the animal to cross the fence. Landowners have successfully used HTEF to enclose bison (*Bison bison*), prevent overuse of riparian areas, and enclose domestic species while allowing crossing by wild ungulates (Karhu and Anderson 2006). Increasing ungulate populations across many portions of the United States have increased concern for overuse of palatable plants, habitat degradation, changes to avian and mammalian communities (Conover 2002), animal-vehicle collisions (Oosenbrug et al. 1991, Romin and Bissonette 1996, Leblond et al. 2007) animal-aircraft collisions (Bashore and Bellis 1982, Wright et al. 1998, Dolbeer et al. 2000, Wright 2001), and spread of disease (VerCauteren et al. 2006). Various fence designs have successfully addressed many of these concerns (VerCauteren et al. 2006).

Despite limited research on white-tailed deer (*Odocoileus virginianus*) populations behind “deer-proof” fences, potential impacts of fences on ungulates are a concern (Demarais et al. 2002). A fence may affect a deer’s home range or movements. Dispersal of yearling male white-tailed deer in southern latitudes (Nelson and Mech 1984, Nixon et al. 1991) and migration movements in northern latitudes are most likely limited by effective fence designs. Home range sizes are often larger than average landholding size (McCoy et al. 2005, Webb et al. 2007), but as long as all basic habitat requirements are met within an enclosure, deer should be able to adapt quickly (Demarais et al. 2002).

Little research has focused on HTEF and the effects on white-tailed deer spatial dynamics and efficacy to control movement. I wanted to evaluate the effect of this low-

cost alternative to traditional fence designs on deer movements. My objectives were to: determine the efficacy of the HTEF to control white-tailed deer movements across property boundaries and evaluate the influence of the HTEF on deer spatial dynamics.

STUDY AREA

I conducted this study on the Samuel Roberts Noble Foundation Wildlife Unit (NFWU) located in southern Oklahoma in Coal, Hughes, and Pontotoc Counties (Figure 2.1). The NFWU was 1,214 ha and is 8.0 km south of Allen, Oklahoma in the Cross Timbers and Prairies ecoregion. A 2.5-m tall, HTEF fence containing 15 smooth wire strands with alternating positive and negative wires was erected around 1,184 ha of the study area (note difference in shape of study area between Figure 2.1 and 2.4). The fence was maintained by 3 high-voltage (4,000-7,000 V) low-amperage (35-50 J or stored energy) energizers. Wires were spaced as follows: first wire was 5 cm above the ground, the next 8 wires were spaced 15 cm apart, and the top 6 wires were spaced 20 cm apart (Figures 2.2 and 2.3). The fence was erected in 1992 to facilitate white-tailed deer management programs and discourage human trespass. The NFWU was approximately 60% wooded and 40% open, with a high degree of interspersion (Gee et al. 1994). During years when global positioning system (GPS) collars were deployed, rainfall ranged from 64.8 to 117.6 cm (Ada, OK; National Climatic Data Center 1999-2005). Average January temperature was 4.8° C and average July temperature was 27.7° C during the study (Ada, OK; National Climatic Data Center 1999-2005).

METHODS

Capture and handling

I captured deer using a drop-net (Ramsey 1968, Gee et al. 1999) baited with corn during winter. I sedated deer using Xylazine (3-6 mg/kg, Phoenix Scientific, St. Joseph, Missouri, USA) or a Telazol[®]-Xylazine mixture (4.4 mg/kg Telazol[®], Fort Dodge Animal Health, Fort Dodge, Iowa, USA, plus 2.2 mg/kg xylazine) and yohimbine (Abbott Laboratories, North Chicago, Illinois, USA) as an antagonist at 0.125 mg/kg. I captured 419 deer and fitted them with plastic livestock ear tags; 35 of these deer (19 females, 16 males) were additionally fitted with a G2000 remote-release global positioning system (GPS) collar (Advanced Telemetry Systems, Isanti, Minnesota, USA) during winter 1998-2004 (Appendix A).

Barrier evaluation

GPS data collection

Global positioning system collars were programmed to collect data during 3 seasons. Twenty collars collected data during spring, 11 during summer, and 7 during winter. A VHF transmitter incorporated into the GPS collars provided data on animal mortality. A GPS fix was attempted every 15 min for approximately 60-75 days. I remotely triggered release of collars after approximately 4 months and downloaded location estimates.

I scrutinized deer location data based on time, number of locations, and accuracy of the GPS system to determine if deer moved across property boundaries. Time (i.e., hr and min) incorporated into collars, distance from the fence, and number of locations were the primary criteria used to determine if a crossing occurred. From 1999-2000, I classified an event as a crossing if ≥ 4 sequential locations occurred >100 m beyond the boundary of the fence because selective availability (i.e., degradation of GPS receiver accuracy) was in effect, which reduced location accuracy (Rodgers 2001). After 2000, ≥ 4 sequential locations ≥ 20 m beyond the fence was classified as a crossing because selective availability was not in effect; therefore, location accuracy increased (Rodgers 2001). I mapped all water gaps, holes, and temporary non-electrified portions of the fence using a differential GPS unit to determine the likelihood that a crossing occurred at one of these locations. Portions of the HTEF were temporarily non-electrified due to excessive vegetation or debris load, flooding, and energizer malfunction.

Tag recoveries

I used tag recovery off the property as a second method of detecting deer movements across the fence. I sexed and tagged all captured deer from 1993-2005 with unique plastic colored and numbered livestock ear tags containing contact information to Noble Foundation employees. Neighboring landowners were asked to report if deer were harvested or recovered on surrounding properties.

Influence of fencing on home range and movements

I used 3 methods to determine effects of the HTEF on deer spatial dynamics. First, I calculated 50 and 95% fixed kernel (FK) (Worton 1989) and minimum convex polygon (MCP) home ranges in Home Range Tools (HRT) for ArcGIS® (Rodgers et al. 2005). I used unit variance standardization and the reference bandwidth smoothing parameter (h_{ref}) when calculating 50 and 95% FK volume probability polygons. I calculated 50 and 95% MCP probability polygons (Kenward 1987) using the fixed mean option (i.e., proximity to mean of all fixes).

Second, I examined how 95% FK and MCP home ranges were associated with the fence by calculating a percentage of fence perimeter in common with the perimeter of each deer's home range. I also calculated the percentage of 50% FK and MCP core area perimeters that were in common with the fence perimeter. For example, the fence perimeter in common with the deer's home range (e.g., 1,000 m) was divided by the total perimeter of the deer's home range (e.g., 5,750 m) and multiplied by 100 to determine the percentage of the HTEF comprising the home range boundary (e.g., 17.4%). The greater the percentage, the more a deer's home range was in association with the fence.

Last, I incorporated movement parameters (rate-of-travel and absolute values of turning angles) to determine if deer movements were influenced by the fence at varying distances (distance class = 0-100, 100-200, 200-300, 300-400, 400-500, 500-600 and >600 m; Figure 2.4) from the fence. I used rate-of-travel and absolute values of turning angles because these movement parameters are typically influenced by the spatial distribution of external factors (e.g., food, mates, predators, habitat, anthropogenic

factors, etc.) (Turchin 1991). Rate-of-travel (m/min) was calculated by subtracting time between successive fixes (elapsed time) and dividing distance moved between successive fixes by elapsed time. Rate-of-travel was calculated instead of distance traveled to standardize variation in sampling interval, which was the result of missed fixes and differences in acquisition time. I also took the absolute value of the turning angle (hereafter just turning angle) because, for example, a 45 degree turn to the right is equivalent to a -45 degree turn to the left. Locations occurring outside of the property boundary were excluded from analyses of rate-of-travel and turning angle.

Statistical analysis

I used a randomized complete block design analysis of variance with deer as blocks to test if mean rate-of-travel or mean turning angle (i.e., response variables) differed by distance class (i.e., treatment). I made multiple comparisons using Tukey's mean separation test when a significant F -test occurred at $P < 0.05$. Homogeneity of variances among distance class (i.e., treatment) was evaluated with the Bartlett's test (Zar 1999). I conducted all analyses using SAS 9.1 (SAS Institute 2003). I concluded statistical significance for $P \leq 0.05$. All means are reported \pm SE.

RESULTS

I analyzed data on 35 deer (19 females, 16 males) with a total of 129,299 GPS locations. I sampled 10 females and 9 males during spring, 8 females and 1 male during summer, and 1 female and 6 males during winter. Collars collected an average of 3,900 locations \pm 355 (SE) over an average of 54 days \pm 3 (SE). Successful locations were obtained in 72% \pm 4 (SE) of attempted fixes.

Barrier evaluation

GPS collars

I found that 8 GPS-collared deer (4 females, 4 males; 23%) crossed through the fence a total of 15 times and returned 13 times. Age of deer crossing the fence ranged from 2 to 7 years. Seven of 8 deer (3 females, 4 males) crossed during spring accounting for 93% of all crossings and 1 female crossed during summer. Two deer crossed through the fence multiple times, one female crossed through the fence 6 times and returned back to the property 5 times during spring. One male crossed through 3 times and returned all 3 times during spring. One male deer crossed the fence during spring and never returned while the GPS collar was collecting data. However, the released collar was recovered within property boundaries.

Fence crossings occurred under a range of conditions and at multiple sites. I mapped 47 and 16 known holes and gaps, respectively and 2 temporarily non-electrified portions of the fence. One crossing (4%) occurred through a non-electrified portion of

the fence, 75% ($n = 21$) occurred at or near a hole or gap, and 21% ($n = 6$) occurred through an electric portion. On average, deer crossed within $88 \text{ m} \pm 23$ (SE; 95% CI: 40-135 m) of a hole or gap. I assumed deer crossing at unknown locations or >135 m from the nearest hole or gap went through the electric strands of the fence. Three deer of 35 (9%) that were found to have crossed the fence went through the electric strands of the fence a total of 6 times.

Tag recoveries

I captured 419 deer (206 females, 213 males) during 1993-2005 within the HTEF. Twenty four of 419 (6%) tagged deer, including collared deer, were found dead or harvested off of the property. Of 206 females, only 4 (2%) were found dead or reported harvested outside of the property boundary. Twenty males of 213 (9%) were either reported harvested or found dead off of the property.

Influence of fencing on home range and movements

Although the majority of deer core areas of use were not associated with the fence, core area size was larger for deer with core areas bordering the fence. Forty percent (14 of 35) and 37% (13 of 35) of core areas of use were associated with the fence using the MCP and FK home range estimators, respectively. Core areas of use associated with the fence were 128% and 21% larger for males and 163% and 88% larger for females than core areas not associated with the fence using MCP and FK estimators, respectively (Table 2.1). An average of $17\% \pm 3$ (SE) and $21\% \pm 3$ (SE) of the length of

core area perimeters were associated with the HTEF when calculated by FK and MCP estimators, respectively.

Home range boundaries of deer came into contact with the HTEF more often than core areas due to their larger size and relatively small study area. Home ranges calculated using MCP and FK estimators were associated with the fence in 83 (29 of 35) and 89% (31 of 35) of the cases, respectively. Similar to core areas, home ranges in association with the HTEF were larger than home ranges not in association with the fence for females and males (Table 2.1). Male home ranges associated with the fence were 245% and 272% larger than home ranges not associated with the fence using MCP and FK estimators, respectively while female home ranges were 29% and 46% larger when in association with the fence. An average of $28\% \pm 3$ (SE) and $34\% \pm 3$ (SE) of the length of home range perimeters were associated with the HTEF when calculated by FK and MCP estimators, respectively.

Quantifying animal movement patterns showed little effect of the HTEF. I found no difference ($F_{6,220} = 1.25$, $P = 0.284$) in turning angles between successive locations among the 7 distance classes from the fence (Table 2.2). I found that rate-of-travel (m/min) differed ($F_{6,220} = 2.43$, $P = 0.027$) among the 7 distance classes from the fence (Table 2.2). Rate-of-travel was greatest >600 m from the fence, similar to rate-of-travel <100 m and 300-600 m from the fence, and greater than 100-300 m from the fence (Table 2.2). Rate-of-travel was similar among all distance classes from 0-600 m (Table 2.2).

I observed incidental crossings and mortalities associated with the HTEF. Five deer (1 tagged, 4 untagged) were found dead still entangled in the fence by their rear legs.

These 5 deer apparently attempted to jump through the strands of the fence. I observed both males and females successfully jump through the wires of the fence while patrolling the perimeter in vehicles and during casual observation. Most deer jumped through after apparently being startled by the vehicle; however, several females were witnessed passing through the fence and one over without any provocation.

DISCUSSION

Fences impact animal behavior (Nielsen et al. 1997, Demarais et al. 2002, Karhu and Anderson 2006, VerCauteren et al. 2006), primarily movements (e.g., dispersal, migration) and home ranges. Level of control, animal behavior, and potential negative effects (VerCauteren et al. 2006) were considered in evaluating the HTEF. My fence design needed to be effective at controlling deer movements, but also needed to have as little influence on deer behavior as possible. I found little evidence of the HTEF having any potentially negative effects on deer behavior.

Deer in my study were not negatively affected by the HTEF because deer were habituated to the fence prior to being radio-collared, as can be seen from the large percentage of deer home ranges associated with the fence. Home range association with the fence, however, was likely an artifact of the relatively small study area size, large perimeter to area ratio (1 km/60 ha), and large home range size of some deer. Because home ranges came into contact with the fence, deer were moving in proximity to the fence. If the HTEF was exerting an influence on deer, either from investigation of the fence or as a learned behavior from a previous negative contact, then movements may

change as deer approach the fence. For example, the greater the movement velocity the more likely an animal is to leave the area while lower turning angles result in more directed animal movement paths. Therefore, if the fence was having a negative effect on deer movements then deer would move at greater velocities along the fence and have more directed movement paths. The fact that I found no difference in turning angle among distance classes or rate-of-travel <100 m from the fence and all other distance categories indicates that movements were not affected by the fence. Thus, it appears as though deer tolerated the electric fence.

When properly maintained the HTEF proved to be an effective deterrent to deer movement. The majority of deer crossings (75%) occurred at gaps or holes; therefore, these areas are a significant source of fence breachment. Nielsen et al. (1997) found openings at road and stream crossing allowed for deer emigration. Moose in Canada were also found to cross at or near an opening in the fence (Leblond et al. 2007). My study area was completely enclosed but had several problem areas, which included water gaps and holes under the fence and temporary periods of no electric current. Because several deer crossed the fence multiple times, it appears that deer were either constantly testing the electric strands for failures or were habituated to crossing at water gaps or holes. The perimeter of the fence should be patrolled on a regular basis to find and fix problem areas, which should reduce crossings since 5 of 8 collared deer crossed at these locations.

It is unlikely I would have been able to detect the level of breachment as accurately as I did if I had not fitted deer with GPS collars. If I had relied on tag

recoveries from outside of the HTEF then I would have underestimated the proportion of deer leaving the property by 17%. One possible explanation for the large difference between the two marking techniques is due to reporting probability of tag recoveries. Reporting probability, as estimated from recapture-resight-recovery data, was relatively low for both sexes. Females harvested or found dead outside of the HTEF were reported 53% of the time compared to 35% of the time for males (S. L. Webb, Mississippi State University, unpublished data).

Differences in reporting rates may be due to differential harvest or dispersal of the sexes where males are more likely to be harvested and disperse than females (Greenwood 1980, Dobson 1982). A lower probability of males being reported, but greater numbers of males reported than females, likely means more males left the property than females or were more susceptible to harvest. Although spring is one of two primary peaks in dispersal of male deer (Nixon et al. 2007), which coincided with collared males leaving the property, only 1 male (~1.8 years) of 4 was likely to disperse when considering yearling males are the sex and age most likely to disperse (Nelson and Mech 1984, Nixon et al. 1991). While the collar was operational, this deer did not exhibit any long-distance movements but rather wandering behavior, which led him off of the property and eventually back on. However, 40-47% of ear-tagged males ≤ 2 years-of-age could have dispersed off of the property because the majority of ear-tagged males were captured as fawns (52%) and yearlings (34%; S. L. Webb, Mississippi State University, unpublished data).

Although my fence design was not completely effective at controlling deer movements, it did control a large percentage of the population. Reduced movements across the fence could still facilitate management without compromising the long-term health of deer. If the goal is to completely enclose or exclude white-tailed deer, then alternative fence designs or modification of the 15-strand HTEF may be needed. Areas in which the HTEF design may not be desirable include animal facilities where enclosed animals are known to harbor disease and around airports where complete exclusion of deer is required. For example, fence-line contact between deer and elk from a captive facility in Wyoming infected with chronic wasting disease may have exposed uninfected, transported elk to the chronic wasting disease prion (Williams et al. 2000). Designs that limit contact and prevent movement through the fence are most desirable. Deer were also found to be the most hazardous wildlife species on airport runways (Dolbeer et al. 2000), threatening human lives and safety and causing substantial economic damage (VerCauteren et al. 2006).

One goal of fence design is cost-effectively limiting access of deer to sensitive habitats, crops, or plant species. Compared to traditional woven wire fences, HTEF are cheaper to build per km in terms of labor and materials. At 2006 costs, construction of a HTEF around the NFWU (19.67 km) would have cost \$195,977 (\$9,963/km) compared to a woven wire fence that would have cost \$275,863 (\$13,947/km). Costs associated with monitoring the fence were not included because monitoring should be equal for any type of fence as long as a particular fence design does not need to be monitored more frequently. However, maintenance costs will differ based on fence design and, in the

case of the HTEF, costs associated with powering the fence will increase long-term costs of the HTEF. Therefore, lower initial costs of the HTEF may be negated by long-term costs of maintenance and supplying electrical power unless sources of solar power are incorporated into fence design. I also found HTEF to be relatively safe, documenting only 5 direct mortalities. For these reasons, the 15-strand HTEF could be an affordable, safe, and successful way of reducing damage by deer with limited negative effects to deer behavior.

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Table 2.1 Core area and home range sizes (ha) for 35 white-tailed deer (19 females and 16 males) bordering and not bordering the 15-strand high-tensile electric fence (height = 2.5 m) on the Samuel Roberts Noble Foundation Wildlife Unit in Oklahoma during 1999-2005. Core area and home range sizes were calculated using the minimum convex polygon (MCP; **A**) and fixed kernel (FK; **B**) estimators.

A

Sex	Fence	<u>50% MCP core area</u>		<u>95% MCP home range</u>	
		N	Mean (SE)	N	Mean (SE)
Female	Yes ¹	7	38.9 (9.8)	15	99.2 (24.7)
Female	No ²	12	14.8 (2.8)	4	76.7 (19.4)
Male	Yes	7	140.8 (32.4)	14	346.8 (36.5)
Male	No	9	61.7 (15.8)	2	100.4 (21.6)

B

Sex	Fence	<u>50% FK core area</u>		<u>95% FK home range</u>	
		n	Mean (SE)	n	Mean (SE)
Female	Yes	6	29.4 (9.7)	16	85.6 (15.8)
Female	No	13	15.6 (2.9)	3	58.6 (10.1)
Male	Yes	7	81.1 (17.5)	15	310.2 (38.1)
Male	No	9	66.8 (12.9)	1	83.4 (--)

Table 2.2 Rate-of-travel (m/min) and absolute values of turning angles in each of 7 distance classes from the 15-strand high tensile electric fence (height = 2.5 m) for 35 white-tailed deer (19 females and 16 males) fitted with GPS collars on the Samuel Roberts Noble Foundation Wildlife Unit in Oklahoma during 1999-2005.

Distance		<u>Rate-of-travel</u> ¹		<u>Turning angle</u> ³
category (m)	n	Mean (SE) ⁴	Mean separation test ²	Mean (SE) ⁴
<100	34	4.6 (0.6)	AB	98.4 (1.9)
100-200	34	3.8 (0.3)	B	98.6 (1.6)
200-300	34	3.9 (0.3)	B	98.9 (2.0)
300-400	35	4.6 (0.4)	AB	97.6 (2.9)
400-500	31	4.3 (0.3)	AB	95.1 (1.9)
500-600	31	4.6 (0.6)	AB	100.4 (4.1)
>600	28	7.2 (1.7)	A	91.1 (3.6)

¹ $F_{6,220} = 2.43, P = 0.027$

²Distance categories with the same letter were not different at $\alpha = 0.05$ for rate-of-travel.

³ $F_{6,220} = 1.25, P = 0.284$

⁴Comparison of means for rate of travel and turning angle among 7 distance categories was tested using a randomized complete block design analysis of variance.

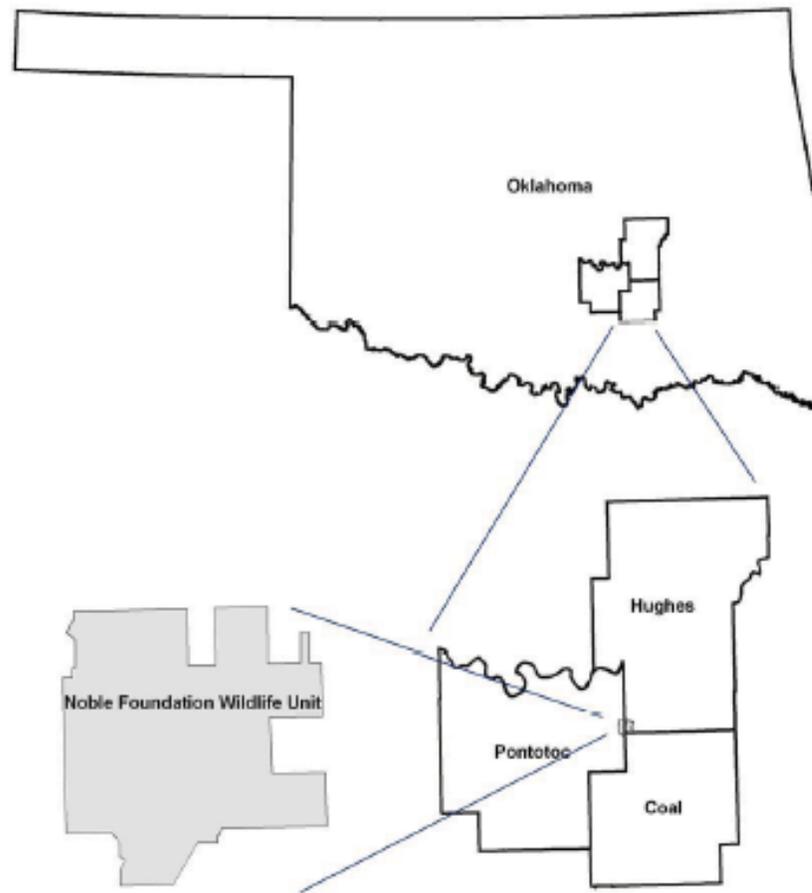


Figure 2.1 Samuel Roberts Noble Foundation Wildlife Unit located in Coal, Hughes, and Pontotoc Counties, Oklahoma, USA.



Figure 2.2 Wire spacing (cm) of a 15-strand high-tensile electric fence (height = 2.5 m) with alternating positive (+) and negative (-) wires constructed around the Samuel Roberts Noble Foundation Wildlife Unit in Oklahoma.



Figure 2.3 Photographs of the 15-strand high-tensile electric fence surrounding the Samuel Roberts Noble Foundation Wildlife Unit in Oklahoma. Height of fence was 2.5 m. Photos by Stephen L. Webb.

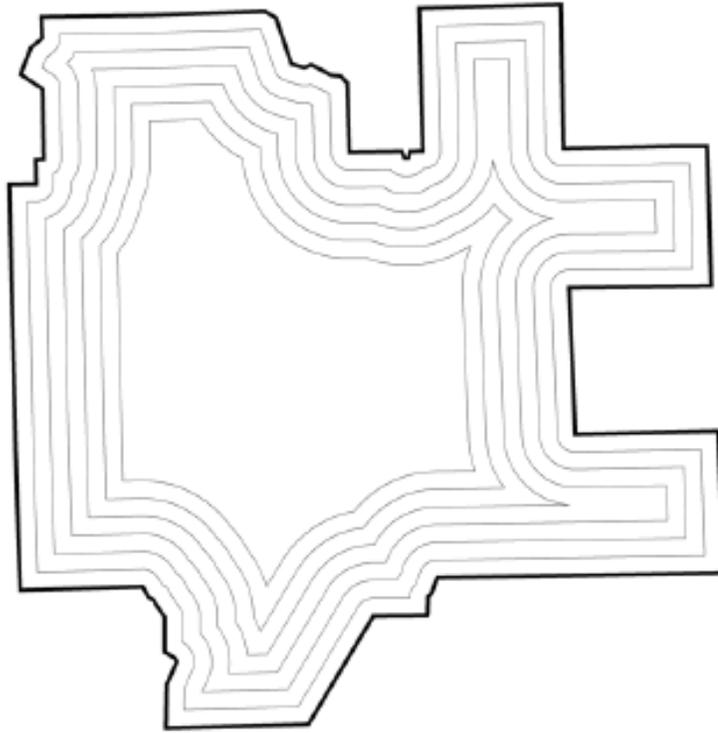


Figure 2.4 Distance classes from the 15-strand high tensile electric fence (height = 2.5 m) at 100 m intervals on the Samuel Roberts Noble Foundation Wildlife Unit in Oklahoma. Bold line represents electric fence; each line inside of the fence represents a 100 m interval (0-100, 100-200, 200-300, 300-400, 400-500, 500-600, >600).

CHAPTER III
MEASURING FINE-SCALE WHITE-TAILED DEER MOVEMENTS AND
ENVIRONMENTAL INFLUENCES USING GPS COLLARS

ABSTRACT

Few studies have documented fine-scale movements of white-tailed deer (*Odocoileus virginianus*) despite the advent of global positioning system (GPS) technology incorporated into tracking devices. I collected fine-scale temporal location estimates (i.e., 15 min/relocation attempt) from 17 female and 15 male white-tailed deer over 7 years and 3 seasons in Oklahoma, USA. My objectives were to: document fine-scale movements of females and males and determine effects of reproductive phase, moon phase, and short-term weather patterns on movements. Female and male movements were primarily crepuscular. Male total daily movements were 20% greater during rut (7,363 m \pm 364) than post-rut (6,156 m \pm 260). Female daily movements were greatest during post-parturition (3,357 m \pm 91), followed by parturition (2,902 m \pm 107), and pre-parturition (2,682 m \pm 121). I found moon phase had no effect on daily, nocturnal, and diurnal deer movements and fine-scale temporal weather conditions had an inconsistent influence on deer movement patterns within season. This study, to my knowledge, represents the largest known sample size of fine-scale white-tailed deer

movements published to date. These data provide useful information into understanding deer movement patterns at temporal scales not previously reported.

INTRODUCTION

White-tailed deer (*Odocoileus virginianus*) movement studies have focused on movements of white-tailed deer at varying spatial scales, from large-scale dispersal and migration to small-scale movements within home ranges and habitats (Webb et al. 2009a). However, few studies have documented fine-scale temporal movements of ungulate species (Pépin et al. 2004), including white-tailed deer, despite the advent of global positioning system (GPS) collars.

A number of factors influence deer movements including reproductive phase, general changes in season and daylength, and environmental influences such as weather. Females alter home range size, mobility, and social interactions (Ozoga et al. 1982; Bertrand et al. 1996; D'Angelo et al. 2004, Webb et al. 2009a). For instance, home range size of females was significantly smaller during parturition periods (14 May-14 July) than during spring (Webb et al. 2009a). Males increase home range size during rut, presumably to search for receptive females (Marchinton and Hirth 1984). However, Webb et al. (2009a) reported no change in home range size but documented increasingly linear movement patterns. Further information is needed to determine if more linear movements are the result of a general change in movement pattern, without a change in movement distance, or due to increased movement distances.

Deer activity relative to environmental factors has been evaluated across the northern U.S. (Progulske and Duerre 1964, Hawkins and Klimstra 1970, Ozoga and Gysel 1972, Zagata and Haugen 1974, McCullough 1982, Beier and McCullough 1990). Less extensive studies (Michael 1970, Kammermeyer and Marchinton 1977, Ockenfels and Bissonette 1982, Ockenfels and Bissonette 1984, Bello et al. 2004) examined broad-scale temporal relationships of white-tailed deer activity and movement patterns to environmental conditions in the southern U.S. However, fine-scale temporal responses to environmental variables are not well known. Winter weather conditions are not as severe in southern climates compared to snow laden northern climates (Teer 1996). However, high temperatures during summer may exert greater influences on deer movement patterns in southern climates. By correlating short-term weather phenomena with fine-scale deer movements I hope to gain insight into the effect of weather on deer movements.

The effect of moon phase on white-tailed deer has received much attention in popular literature (Alsheimer 1999). Some scientific studies of moon phase and deer activity have used visual observations (Buss and Harbert 1950, Michael 1970, Zagata and Haugen 1974), which could have been affected by visibility of the deer and human disturbance. Several other studies (Kammermeyer 1975, Kufeld et al. 1988, Beier and McCullough 1990) used radio telemetry to relate activity rates or movements to moon phase with varied results. Studies quantifying animal activity or movement are few; thus, more data are needed to test this “moon phase hypothesis.” It may be possible that GPS

collar technology can reveal associations between moon phase and movements due to finer resolution of movement distance.

Using fine-scale temporal data, I documented the effects of reproductive phase, weather, and moon phase on deer movements at a temporal scale not previously reported for white-tailed deer. My objectives were to: 1) estimate and compare fine-scale movements of females and males 2) document and compare movements of females during parturition and males during rut, 3) determine the effects of moon phase on deer movements, and 4) determine the effects of short-term weather patterns on deer movements. Because my main objective was to document fine-scale movements of deer as accurately as possible, I used a short sampling interval (Reynolds and Laundré 1990). I hypothesized that females and males would show similar trends in movement patterns during spring because both sexes would be concentrating on foraging to meet metabolic requirements for fawn production and antler growth, respectively. I hypothesized that movements of females during summer would decrease due to parturition and care of young and movement of males during winter would increase due to searching behaviors associated with breeding. Last, I hypothesized that moon phase and weather would have relatively little influence on deer movements because seasonal weather conditions are less severe in southern latitudes.

STUDY AREA

I conducted this study on the Samuel Roberts Noble Foundation Wildlife Unit (NFWU) located in southern Oklahoma in Coal, Hughes, and Pontotoc Counties (Figure

3.1). The NFWU is 1,214 ha in size and is 8.0 km south of Allen, Oklahoma in the Cross Timbers and Prairies ecoregion. A 2.5-m tall, high-tensile electric fence (HTEF) containing 15 smooth wire strands with alternating positive and negative wires was erected around 1,184 ha of the study area. The HTEF was not a complete barrier to deer movements. Tagging and GPS collar studies found deer passed through the fence and home ranges and movements were minimally affected by its presence (Webb et al. 2009a, Webb et al. 2009b). The NFWU is approximately 60% wooded and 40% open, with a high degree of interspersion (Gee et al. 1994). During years when collars were operational, rainfall ranged from 64.8 to 117.6 cm (Ada, OK; National Climatic Data Center 1999-2005). Average January temperature was 4.8° C and average July temperature was 27.7° C during the study (Ada, OK; National Climatic Data Center 1999-2005).

METHODS

Capture and handling

I captured deer using a drop-net (Ramsey 1968, Gee et al. 1999) baited with corn during winter and a tranquilizer dartgun (Pneu-Dart, Inc., Williamsport, Pennsylvania, USA) during fall. I sedated deer using Xylazine (3-6 mg/kg, Phoenix Scientific, St. Joseph, Missouri, USA) or a Telazol[®]-Xylazine mixture (4.4 mg/kg Telazol,[®] Fort Dodge Animal Health, Fort Dodge, Iowa, USA, plus 2.2 mg/kg xylazine) and used yohimbine (Abbott Laboratories, North Chicago, Illinois, USA) at 0.125 mg/kg or

tolazine at 0.4 mg/kg as an antagonist to the xylazine. I captured and fitted 38 deer (21 females, 17 males) with a G2000 remote-release global positioning system (GPS) collar (Advanced Telemetry Systems, Isanti, Minnesota, USA) and plastic livestock ear tags during fall 1998-2004 (Appendix A).

Data collection

GPS location fixes

I programmed GPS collars to collect data during 3 seasons: spring (March-May; n = 20), summer (June-August; n = 11), and winter (November-February; n = 7). A GPS fix was attempted every 15 min for 60-75 days, which would result in 4 fixes/hr. Hereafter, I refer to the distance traveled between 2 fixes as a movement. Four movements are possible/hr by using all fixes within an hour and the first fix of the following hour. I remotely triggered release of collars after approximately 4 months and downloaded location estimates.

Moon phase

I used proportion of the moon's surface illuminated, which is a quantitative measure of the moon's appearance, as a surrogate for moon phase, similar to the approach of Beier and McCullough (1990). Percentage illumination is calculated as area illuminated divided by total moon area multiplied by 100. I did not differentiate between waxing and waning crescent or gibbous phases or between first and last quarters. I

classified moon phase as: new (0.0-0.05), crescent (0.2-0.3), quarter (0.45-0.55), gibbous (0.7-0.8), and full (0.95-1.0). If moon phase did not fall into one of the aforementioned phases it was grouped into an “other” category. Astronomical data were downloaded from the United States Naval Observatory website (<http://www.usno.navy.mil/USNO>).

Weather conditions

I obtained weather data from the Oklahoma Mesonet system, a network of environmental monitoring stations (<http://www.mesonet.org/>). The network consists of over 110 automated stations with at least one station in each of Oklahoma's 77 counties. Environmental conditions, measured every 5 min, are recorded at the Oklahoma Climatological Survey. I obtained mean hourly estimates of air temperature (°C), wind speed (m/sec; 1 m/sec = 3.6 km/hr), pressure (millibars), relative humidity (%) and total precipitation (mm).

Analysis

Hourly movements

I determined total hourly distance travelled by adding straight-line distances between successive fixes within deer. I calculated a mean distance traveled by hour for each deer and used these means to calculate an overall mean of hourly movements by sex and season. Due to the short time interval, I only used deer with all 4 movements/hr. I used a 2-sample *t*-test, assuming equal variances, to compare hourly movement distance

between females and males during spring, females during spring and summer, and males during spring and winter.

Effects of reproductive phase

Mean conception occurred 30 November \pm 1.5 days (SE; range = 4 November-24 December) and mean parturition occurred 15 June \pm 1.5 days (SE; range = 23 May-12 July; Webb et al. 2009a). To avoid the influence of very early or late conceptions on mean conception date, I defined reproductive seasons according to the frequency of conceptions by week. I defined the parturition period into 3 phases similar to Webb et al. (2009a): pre-parturition (14 May-7 June), parturition (8 June-22 June) and post-parturition (23 June-14 July). Based on conception dates the rut was partitioned into 2 phases: rut (18 November-1 December) and post-rut (2 December-23 December). No males were tracked prior to the beginning of the rut phase.

To evaluate differences in total daily deer movement by reproductive season, I used a repeated measures design (PROC MIXED, SAS Institute 2003) with day as a repeated measure and deer as subject, which specifies the unit within which observations are correlated (Littell et al. 2006). I selected covariance structures using restricted maximum likelihood and Akaike information criterion corrected for sample size (AICc; Burnham and Anderson 2002). Based on model results, I used a first order autoregressive covariance structure for females and a compound symmetry covariance structure for males.

Diurnal/nocturnal movements

I downloaded sunrise and sunset data from the nearest location to the study area from the United States Naval Observatory website to determine diurnal and nocturnal movements. Diurnal hours were calculated as the hour of sunrise to the hour of sunset and nocturnal hours as the next hour after sunset and the last hour before sunrise. Deer with ≥ 2 movements/hr within time period were used in these analyses. A diurnal:nocturnal movement ratio (D:N; Kurz and Marchinton 1972) was also calculated from movement rates within diurnal and nocturnal periods. Diurnal:nocturnal ratios < 1 indicate greater nocturnal movements and $D:N > 1$ indicates greater diurnal movements. Movement rates were used to calculate D:N ratios instead of movement distance to account for variations in daylength.

Moon phase

To test for effects of moon phase, time period (i.e., diurnal and nocturnal) and moon phase x time period interaction on sex and seasonal deer movement rates (response variable) I ran a 2-way repeated measures ANOVA (PROC MIXED, SAS Institute 2003) with moon phase as a repeated measure and deer as subject. Movement rate was the metric used in ANOVA due to unequal hours within time period. I used a compound symmetry covariance structure.

Weather

To determine the effect of weather conditions on deer movement patterns within their normal activity rhythms, I totaled the distance moved within each of 4 3-hr time periods using only deer with all 12 movements/time period. Analyzing data during each 3-hr time period allowed me to relate deer movements to actual weather during that time period. Morning movement period was defined as 0600-0800 hr for females during spring and summer and for males during spring and from 0700-0900 hr for males during winter. Mid-day movement period was 1200-1400 hr for females and males during all seasons. Evening movement period was defined as 1700-1900 hr for females during spring and males during spring and winter, and 1900-2100 hr for females during summer. Midnight movement period was from 0000-0200 hr for females during spring and males during spring and winter, and 0100-0300 hr for females during summer.

To assess whether each weather variable was related to movements, I used general linear models with repeated measures (PROC MIXED, SAS Institute 2003) to calculate parameter estimates by sex, season, and time period with day as a repeated measure and deer as subject. I used a spatial power covariance structure for my models.

Despite having sufficient sample size and power to detect general linear relationships, I also considered potential non-linear effects extreme weather conditions may have on deer movements. I calculated z-scores (PROC STANDARD, SAS Institute 2003) based on standard deviations from the mean for each of the 5 independent weather variables during times specified for each sex, season and time period. I used a repeated measures ANOVA (PROC MIXED, SAS Institute 2003) with time period (i.e., morning,

midday, evening, or night) as a repeated measure and deer as subject to compare movement rates of deer during periods of extreme weather (i.e., low and high) and normal weather. I compared deer movements that occurred when weather conditions were ≥ 1 SD above the mean, ≤ 1 SD below the mean, and between the 2 extremes (i.e., -1 to 1) for each weather variable. Assuming normal distributions of weather variables, 68% of observations would fall within ± 1 SD of the mean leaving 16% of observations above and below 1 SD of the mean, respectively. Data were analyzed by sex, season, and time period to account for sex, season, and time period specific movements. Because precipitation did not deviate below 1 SD from the mean I compared movements during extreme highs in precipitation to movements during periods of no precipitation. I used a compound symmetry covariance structure for my models. When a significant *F*-test occurred, I used Tukey's mean comparison test to compare among weather conditions.

To determine if diel changes in weather conditions influenced movement patterns I calculated differences in weather conditions from 1 day to the next within the middle hour for each of the 4 aforementioned movement periods. I used a repeated measures ANOVA (PROC MIXED, SAS Institute 2003) with hour as a repeated measure and deer as subject to compare movement distances of deer among 7 equidistant categories relating to changes in pressure (-10.4 - -7.1 ; -7.2 - 3.9 ; -4.0 - -0.7 ; -0.8 - 2.3 ; 2.4 - 5.5 ; 5.6 - 8.7 ; 8.8 - 12.3), precipitation (-13.8 - -9.8 ; -9.9 - 5.9 ; -6.0 - -2.0 ; -2.1 - 1.7 ; 1.8 - 5.6 ; 5.7 - 9.5 ; 9.6 - 13.8), temperature (-10.2 - -7.5 ; -7.6 - 4.9 ; -5.0 - -2.3 ; -2.4 - 0.1 ; 0.2 - 2.7 ; 2.8 - 5.3 ; 5.4 - 8.1), wind speed (-2.8 - 1.9 ; -2.0 - -1.1 ; -1.2 - -0.3 ; -0.4 - 0.3 ; 0.4 - 1.1 ; 1.2 - 1.9 ; 2.0 - 2.8), and relative humidity (-25.3 - -18.0 ; -18.1 - -10.8 ; -10.9 - -3.6 ; -3.7 - 3.4 ; 3.5 - 10.6 ;

10.7-17.8; 17.9-25.1). Data were analyzed by sex, season, and hour to account for sex, season, and hour specific movements while using a compound symmetry covariance structure for my models.

All statistical analyses were conducted using SAS 9.1 (SAS Institute 2003). I used an *a priori* $\alpha = 0.05$ for statistical tests. All means are reported with standard error (\pm SE) unless otherwise noted. For all repeated measures designs and mixed models I used a degrees of freedom adjustment developed by Kenward and Roger (1997). The Kenward-Roger option accounts for unbalanced data, multiple random effects, and any model with correlated errors (Littell et al. 2006). I examined plots of residuals and normal probability plots to evaluate normality assumptions.

RESULTS

Collar performance

I excluded data from 6 deer due to collar malfunctions (3), short tracking periods of <7 days (1), and small sample size for females during winter (1) and males during summer (1). I analyzed data on 32 of 38 (9 females and 9 males during spring, 8 females during summer, and 6 males during winter) deer for a total of 130,098 GPS locations. On average, collars collected 4,065 locations (\pm 354) for an average of 54 days (\pm 3). Mean number of movements/day was 79 ± 0.3 (95% CI: 78.7-80.1), which was within 95% of total distance travelled if all 96 movements were used. Deer with 48-59 movements/day accounted for <10% of all observations.

Hourly movements

During spring, both sexes exhibited 2 primary peaks in movement from 0600-0800 hr and again from 1700-1900 hr, which closely corresponded with sunrise and sunset (Figure 3.2a-b). Peaks in movements began at sunrise and 2 hours prior to sunset (Figure 3.2a-b). Female movements ranged from a low of 177 m (± 28) at 0200 and 177 m (± 31) at 1400 hr to a high of 357 m (± 38) at 0700 hr. Male movements ranged from 169 m (± 29) at 1100 hr to 403 m (± 23) at 1800 hr. I found no difference in hourly movement distance between females and males during any hour in spring ($P \geq 0.151$).

Peak movements by females during spring were more distinct than during summer. Summer hourly movements were about 150 m per hr (Figure 3.3a). Movements increased after sunrise, with peak movements occurring at 1200 hr (210 m \pm 48) and just before sunset with another peak at 2000 hr (210 m \pm 36) whereas movement was lowest at 0300 hr (95 m \pm 12; Figure 3.3a). Female movements during spring exceeded movements during summer 50% of the time and were similar the other 50% of the time. Movements during spring were greater at 0200-0300, 0500-0800, 1100, 1300, and 1600-1900 hr ($P \leq 0.034$).

Males in winter predominately moved during 0700-0900 hr and from 1700-1900 hr, immediately after sunrise and sunset, respectively (Figure 3.3b). Decreased movements occurred from 1200-1500 hr (Figure 3.3b). Movement was greatest at 0700 hr (436 m \pm 55) and least at 1200 hr (131 m \pm 19; Figure 3.3b). I found male movement distance differed from spring and winter for 5 of 24 hours. Males moved greater distances from 0500-0600 hr and 1900 hr during spring compared to winter ($P \leq 0.041$).

At 0900 and 1700 hr male movements were greater during winter than spring ($P \leq 0.047$).

Effects of reproductive phase

Female daily movements varied by parturition period ($F_{2,63.3} = 3.35$, $P = 0.041$). Female daily movements were lowest during pre-parturition (2,682 m \pm 121; 95% CI: 2,438-2,926) followed by parturition (2,902 m \pm 107; 95% CI: 2,690-3,114). Female daily movements during post-parturition (3,357 m \pm 91; 95% CI: 3,176-3,538) were 25% and 16% greater than pre-parturition and parturition, respectively. Movements among females were also less variable; therefore, females appeared to respond similarly to parturition periods.

Male daily movements did not differ between rut and post-rut ($F_{1,144} = 3.33$, $P = 0.07$). However, daily movements during rut (7,363 m \pm 364; 95% CI: 6,633-8,093) were 20% greater than during post-rut (6,156 m \pm 260; 95% CI: 5,639-6,673), which represents a significant change in movement patterns from a biological perspective. Male movements were more variable during the rut, which may indicate different search patterns for receptive females.

Moon phase

The main effect of time period (i.e., diurnal and nocturnal) influenced female movement rate during spring ($F_{1,699} = 13.74$, $P < 0.001$) and summer ($F_{1,610} = 42.39$, $P < 0.001$; Table 3.1). Male movement rate was also influenced by time period during spring

($F_{1,746} = 4.06$, $P = 0.044$) and winter ($F_{1,684} = 10.96$, $P = 0.001$; Table 3.1). The main effect of moon phase had no influence on movement rates ($P \geq 0.153$) or the interaction between time period and moon phase ($P \geq 0.249$). After accounting for daylength, female movement rates and male movement rates during winter were greater during nocturnal hours (i.e., D:N ≤ 0.98 ; Table 1). However, male movement rates during spring were greater during daylight hours (D:N = 1.04; Table 3.1).

Weather

I found general linear trends in movements related to 4 of the 5 weather variables in only 8 of 80 (10%) models (Table 3.2). Temperature influenced movements in 5 of 8 cases and rain, relative humidity and wind speed each in 1 case (Table 3.2). Parameter estimates of the 8 significant models do not provide useful biological meaning as all parameter estimates were ≤ 29 m/hr, which partially may be due to collar error or tortuosity of movement paths at short time intervals. Overall, there was no apparent trend ($P \geq 0.062$) of weather effects on movements of either sex during any season or time period (Table 3.2).

I extracted lower, normal, and upper weather conditions, based on deviations from normal patterns, by sex, season, and time period to determine how movements differed among weather conditions and to detect non-linear relationships (Table 3.3). I found differences among movement categories relative to weather conditions in 11 of 80 (13.8%) models. Temperature accounted for most (6 of 11; 55%) differences in movements, followed by relative humidity (3), precipitation (1), and wind speed (1).

Atmospheric pressure had a weaker influence on period-specific movements ($P \geq 0.061$) for females or males. Male movements during spring evenings were greater (844 ± 133 m) during above-normal precipitation compared to normal (519 ± 50 m; Table 4).

Relative humidity affected females on one occasion with females moving more during periods of high relative humidity whereas male movements were greater when relative humidity was lowest (Table 3.4). Movements of both females and males across seasons revealed greater movements when temperatures were lowest except on 1 occasion when movements were greater during normal temperatures (Table 3.4). Last, wind speed influenced male movements during spring evenings. Movements were greater during low wind speeds ($1,330 \pm 104$ m) compared to high wind speeds (942 ± 113 m; Table 3.4). Overall, there was no general pattern in how weather influenced deer movements except that temperature influenced deer movements more than any other weather variable.

Changes in weather patterns within hour from 1 day to the next affected movements in 10 of 80 models (12.5%). Temperature, relative humidity and wind speed each affected movements in 2 instances, whereas precipitation and pressure affected movements in 1 and 3 instances, respectively. Movements were primarily affected by changes in weather during hours of limited movements (i.e., 0100-0200, 1300). Female movements during spring (0100 hr) were relatively stable except when temperature increased $>5.4^{\circ}\text{C}$ from one day to the next (Figure 3.4a) whereas male movements during winter (1300 hr) gradually increased with rising temperatures (Figure 3.4b). Movements of males during spring exhibited 2 patterns depending on time of day in relation to relative humidity. Movements were least at 0100 hr when relative humidity changed

most drastically in either direction (Figure 3.4c) whereas movements at 1300 hr were greatest when relative humidity increased most (Figure 3.4d). Precipitation only affected females during summer at 1300 hr. Movement was greatest after heavy rains (i.e., decreasing rainfall) then gradually decreasing as rainfall increased until large amounts of precipitation resulted in greater movement distance (Figure 3.4e). Pressure had no clear effect on deer movements. Female movements were greatest during spring when pressure dropped (Figure 3.4f) whereas male movements during winter were greatest when pressure increased dramatically (Figure 3.4h). However, movements were relatively stable over most pressure changes for both sexes (Figures 3.4f-h). Similar to relative humidity, wind speed affected males differently during winter depending on time of day. Movements were greatest at 1300 hr when wind speed decreased (Figure 3.4i) while movements at 1800 hr were greater when wind speeds decreased and increased most dramatically (Figure 3.4j).

DISCUSSION

My frequent fix schedule allowed me to model fine-scale temporal movements of deer and examine influences of short-term weather phenomena and moon phase on deer movements. Movements may be underestimated when movement paths are tortuous or fix intervals are long (Mills et al. 2006). Previous research found that deer movement paths were tortuous (Webb et al. 2009a). However, my fix schedule (4 movements/hr or 2 movements/hr) likely captured realistic movement distances. My study also had the advantage of recording locations at 15-min intervals compared to previous studies which

used “bursts” of telemetry locations to sample hourly or daily distance moved. Because my data were frequent and not limited by sampling intensity, I more accurately represented movement patterns across periods of interest.

Similar to previous research, I found white-tailed deer primarily were crepuscular (Michael 1970, Kammermeyer and Marchinton 1977, Beier and McCullough 1990), with greatest movements occurring near sunrise and sunset. Although movement may be similar across seasons, the purpose of movements may change. Therefore, changes in daily movement across seasons can reflect physiological changes within the animal or environmental changes.

Long time periods, such as seasons or years, may mask fine-scale movement patterns. Subdividing seasons into biological seasons pertaining to breeding, revealed changes in daily movement patterns. Previous studies found that parturition influenced home range size, movement, and social interactions (Ozoga et al. 1982; Bertrand et al. 1996; D’Angelo et al. 2004, Webb et al. 2009a). I also found that reproductive period influenced female movements. Movements were greater during post-parturition, which may be influenced by increased fawn mobility or increased energy requirements due to demands from lactation. Increased energy demands may require females to move farther between foraging patches. Another analysis of my data showed that female home range size was significantly less during summer compared to spring and movements of females were more tortuous, likely due to being confined to a smaller area (Webb et al. 2009a).

Male deer also appear to change their daily movement patterns in response to breeding period (i.e., rut and post-rut). Marchinton and Hirth (1984) found that males

will increase home range size during rut. However, home range size between the rut and spring periods were similar for males on the NFWU (Webb et al. 2009a). Males appear to confine movements to previously established home ranges during the rut (Hellickson et al. 2008, Webb et al. 2009a) but may change their activity (Hellickson 2002) or movements patterns within home ranges based on fractal analyses (Webb et al. 2009a). I found males also changed their movement patterns by increasing movements during the rut compared to post-rut. This finding corroborates the finding that male movements during rut were more linear, which may have resulted from increased movement distance. Therefore, confining movements to the home range may provide protection and security as evidenced by high annual home range fidelity (Webb et al. 2007a, Hellickson et al. 2008). Changing movement patterns within home ranges may also be due to responses for available resources (e.g., receptive females, forage, etc.), which will vary based on physiological state and condition and habitat quality.

Few studies have documented changes in diurnal and nocturnal movements across seasons. A study in Georgia revealed female deer moved twice as far during diurnal hours than nocturnal hours (Kammermeyer and Marchinton 1977). However, the D:N ratio reported was partially influenced by increased daylength. I found much lower D:N ratios because I accounted for number of hours within each time period. Therefore, researchers should consider using other possible movement parameters, such as movement rate, to account for discrepancies in daylength.

Female nocturnal movements during summer were greater than diurnal movements. However, in general, movements during summer were reduced compared to

spring. Environmental temperature may influence activity rhythms in animals (Randall et al. 2002); thus, changes in female movements during summer may be related to environmental conditions. However, my data indicated that environmental variation exerted minimal influence on deer movements at fine temporal scales within season. Therefore, changes in female movements from one season to the next may reflect changes in physiological state or acclimatization to seasonal conditions. Females appeared to adjust time budgets relative to movements. Movements generally were reduced during summer and increased at night, which may be a behavioral adaptation (Randall et al. 2002) to reduce heat stress. Because general movement patterns were changed during summer, weather had little influence on fine-scale temporal movements within this season.

I observed a large decrease in diurnal male movements (i.e., $D:N < 1$) during winter compared to spring. Males in my study may have become more nocturnally active in winter due to hunting or the rut, both of which occurred during the winter season. Female deer were found to be less active during the hunting season during diurnal hours compared to nocturnal hours and the non-hunting season (Kilgo et al. 1998). Males in this study may have responded in a similar fashion by decreasing daytime movements to avoid contact with hunters. Males may also have changed movement patterns due to rut. If females were more active at night during hunting season as found by Kilgo et al. (1998), and since hunting season typically coincides with the breeding season and when females are in estrous on the NFWU, then it follows that male movement patterns during that time period may be similar to that of females. Unfortunately, I had no data for

females during the rut, which makes examination of the 2 causes for changes in male movement patterns difficult.

The aforementioned explanations for nocturnal movement may outweigh the costs of increases in metabolic rate during cold temperatures due to thermoregulation and activity (Gates and Hudson 1979). Activity, or movement in the present study, could be a thermoregulatory penalty during cold weather that increases with increasing activity (Gates and Hudson 1979). If this were true, deer should avoid moving at night during winter when temperatures are lowest to avoid increased metabolic rate. Because I did not find this to be true, temperature extremes in southern Oklahoma may not be cold enough for deer to be metabolically stressed to a point where compensation for increased metabolic rate could not be recovered. However, male deer voluntarily reduce forage intake during rut, which may not allow them to meet metabolic requirements. Increased movements and decreased forage intake during rut offer additional support for increased rut-related mortalities in males (Ditchkoff et al. 2001, Webb et al. 2007b).

Increasing moon phase generally results in decreased nocturnal activity or movements for many species (e.g., Bowers 1988, Gilbert and Boutin 1991, Cresswell and Harris 1988, Julien-Laferrière 1997, Erkert 1989). However, an observational study of mule deer (*Odocoileus hemionus*) occurrence at salt licks found that visitation to salt licks was highest during full moons (Buss and Harbert 1950). Observational studies of white-tailed deer (Michael 1970, Zagata and Haugen 1974), however, found that moon phase had no effect on number of deer sighted. I concur with the speculation of Zagata and Haugen (1974) that the increase in deer sightings during full moons by Buss and

Harbert (1950) may have been due to an increased observer ability to see during full moons and not an effect of moon phase itself. Observational studies are confounded by a number of factors such as visibility, vegetation types, time of day, and observer presence. Without the aid of night-vision optics, which were not available during earlier studies, deer would have been hard, if not impossible, to count during new moons. Due to limitations of observational studies, studies that remotely monitor animal movement or activity (e.g., activity collars and dataloggers; VHF telemetry; GPS collars) are preferred.

Previous studies have used variable-pulse activity sensors to monitor white-tailed deer (Beier and McCullough 1990, Hellickson et al. 2007) and mule deer (Kufeld et al. 1988) activity patterns relative to moon phase. None of the aforementioned studies found an affect of moon phase on deer activity patterns. These findings are similar to my current findings; moon phase had no influence on deer movement patterns.

There is much conflicting evidence on the affects of weather on deer activity and movements (Kammermeyer and Marchinton 1977, Marchinton and Hirth 1984, Beier and McCullough 1990, Hellickson et al. 2007). Most studies have found minimal influence of weather on deer activity and movements except during certain seasons or environments. However, the 2 weather factors that consistently affected deer activity and movements, primarily in northern latitudes, were snow depth and temperature (Loveless 1964, Progulske and Duerre 1964, Rongstad and Tester 1969, Moen 1976, Beier and McCullough 1990). These factors are not as important to deer in southern latitudes, except for short periods.

It is difficult to determine the full effect of weather on deer movements because weather and movements both are correlated with seasonal movement patterns (White and Garrott 1990), predator activity, feeding (Beier and McCullough 1990), or breeding. However, my analysis approach allowed me to examine the influence of weather on deer movements within seasons and time periods removing much of the seasonal and daily variation in weather. In general, I found minimal evidence that weather influenced deer movements. Relationships were weak and parameter estimates were small revealing little biological significance in changes in movement distance with changes in weather. Deviations from normal, seasonal weather conditions did not reveal consistent patterns for changes in movement. Interestingly, fine-scale temporal changes in weather over a 24-hr period revealed movements during non-peak movement periods (i.e., midday and night) were affected, whereas periods of normal deer movements (i.e., crepuscular movements) were not affected. Therefore, deer in the southern United States may not be as affected by weather as deer from northern latitudes, which experience more extreme weather conditions (e.g., snowfall, prolonged temperatures $<0^{\circ}$ C). Thus, deer tend to maintain normal, crepuscular movement patterns regardless of weather conditions.

Temperature was the one weather variable showing any consistent effect on deer movements. Behavioral responses of deer may occur when environmental temperatures during summer are greatest or least during winter. Mule deer in an arid rangeland in Washington spent less time active and sought shade during hot weather $\geq 25^{\circ}$ C (Sargeant et al. 1994). However, female deer in this study moved greater distances during summer at times with normal to high temperatures and less when temperatures were coolest.

Although female deer moved more during warmer temperatures of summer, movements in general were less than other seasons, which likely reduced heat stress from a general change in seasonal movement patterns or habitat type. Males during winter moved more when temperatures were lowest. Males may have moved more during winter evenings when temperatures were reduced in preparation of further drops in temperature during night. Therefore, males may have foraged more intensively or moved longer distances during the evening to reach favorable thermal habitats.

Estimation of total daily movements based on limited relocations may lead to erroneous conclusions and gross underestimation of movements. I considered location errors to be negligible relative to a deer's ability to move greater distances than the average error of collars. Effects of GPS collar error on estimated movements should be minimal for species capable of moving long distances compared to the potential GPS collar error during the fix interval (Mills et al. 2006). Previous research found that real daily distance travelled could be obtained with a sampling interval of 0.5 hours (Reynolds and Laundré 1990, Pépin et al. 2004). Therefore, my cut-off of 48 movement segments per day or 2 movements/hr was justifiable to capture an accurate picture of distance travelled.

My results show that deer are crepuscular with regards to movement patterns and that moon phase and weather had an inconsistent influence on movements. Therefore, deer likely maintained normal movement patterns during adverse environmental conditions by seeking favorable habitats. Habitats favorable for thermoregulation should thus be protected and managed for. Additionally, movement patterns of deer may dictate

when and what type of deer survey to conduct (Beier and McCullough 1990) because deer will be more visible during particular time periods. Surveys (e.g., spotlight, aerial, or line) should be conducted when deer movement is greatest. While weather did not influence movements, it may influence habitat use, which should be accounted for in survey design and could account for annual fluctuations in population estimates. Increased movements by males during rut may increase their susceptibility to harvest. Management and harvest plans designed with deer movement patterns in mind may increase overall success of population management goals.

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Table 3.1 Seasonal diurnal and nocturnal hourly movement rates (m) and diurnal: nocturnal movement ratio (D:N) of female and male white-tailed deer on the Samuel Roberts Noble Foundation Wildlife Unit in southern Oklahoma during 1999-2005. n = number of observations.

Sex	Season	n	Time period	Mean (SE)	95% CI		D:N
					Lower	Upper	
Female	Spring	373	Nocturnal	219 (6)	207	230	0.98
		348	Diurnal	215 (6)	204	226	
	Summer	312	Nocturnal	140 (3)	134	147	0.79
		313	Diurnal	111 (2)	106	115	
Male	Spring	389	Nocturnal	202 (4)	193	210	1.04
		377	Diurnal	210 (4)	202	218	
	Winter	363	Nocturnal	262 (7)	248	276	0.87
		341	Diurnal	228 (7)	214	241	

Table 3.2 Linear relationships between weather variables and female and male white-tailed deer movements (m) across seasons and time periods on the Samuel Roberts Noble Foundation Wildlife Unit in southern Oklahoma during 1999-2005.

Sex	Season	Period	Variable	Intercept	Estimate	SE	df	<i>F</i>	<i>P</i>
Female	Spring	Morning	Temperature	1,112.6	-14.70	7.21	136	4.15	0.044
		Night	Precipitation	613.9	87.05	38.95	351	4.99	0.026
	Summer	Evening	Relative Humidity	1,203.6	-8.81	4.12	183	4.58	0.034
Male	Spring	Evening	Temperature	1,351.8	-20.37	5.67	141	12.91	<0.001
		Midday	Temperature	820.7	-17.72	5.73	124	9.57	0.002
	Morning	Temperature	1,441.8	-39.49	6.58	137	36.03	<0.001	
		Wind speed	1,228.3	-68.44	33.36	202	4.21	0.042	
	Winter	Night	Temperature	673.4	13.67	6.85	167	3.98	0.048

Table 3.3 Means (\pm SD) of temperature ($^{\circ}$ C), relative humidity (%), wind speed (m/sec), precipitation (mm), and pressure (millibars) during each respective season and time period during 1999-2005. Means \pm SD were used to compare movements during extreme weather events. n = number of observations.

Sex	Season	Time period	n	Temperature		Humidity		Wind speed		Precipitation		Pressure	
				Mean \pm SD	Mean \pm SD	Mean \pm SD	Mean \pm SD	Mean \pm SD	Mean \pm SD	Mean \pm SD	Mean \pm SD		
Female	Spring	Morning	397	10.75 \pm 5.25	81.34 \pm 9.0	3.24 \pm 1.02	0.2 \pm 0.84	992.11 \pm 5.12					
		Midday	287	18.14 \pm 5.26	56.78 \pm 15.8	4.48 \pm 1.23	0.09 \pm 0.44	990.39 \pm 4.96					
		Evening	378	16.38 \pm 5.23	61.82 \pm 14.48	3.34 \pm 1.08	0.16 \pm 0.87	989.79 \pm 5.01					
Female	Summer	Night	465	11.85 \pm 5.53	82.82 \pm 9.07	2.58 \pm 1.25	0.07 \pm 0.41	990.51 \pm 4.93					
		Morning	282	22.74 \pm 1.87	88.51 \pm 4.31	2.37 \pm 0.95	0.35 \pm 1.22	990.92 \pm 2.51					
		Midday	264	28.6 \pm 2.71	64.93 \pm 10.55	3.3 \pm 0.84	0.14 \pm 0.63	989.6 \pm 2.9					
Female	Summer	Evening	288	24.02 \pm 2.31	83.8 \pm 4.72	1.55 \pm 0.69	0.0 \pm 0.02	988.83 \pm 2.63					
		Night	319	20.8 \pm 2.34	92.44 \pm 3.39	1.65 \pm 0.95	0.14 \pm 0.74	989.09 \pm 2.89					

Table 3.3 Continued.

Sex	Season	Time period	n	Temperature		Humidity		Wind speed		Precipitation		Pressure	
				Mean \pm SD	Mean \pm SD	Mean \pm SD	Mean \pm SD	Mean \pm SD	Mean \pm SD	Mean \pm SD	Mean \pm SD		
Male	Spring	Morning	363	10.9 \pm 5.51	80.54 \pm 8.85	3.26 \pm 1.16	0.12 \pm 0.69	992.28 \pm 5.13					
		Midday	326	18.46 \pm 5.03	54.44 \pm 13.4	4.76 \pm 1.27	0.09 \pm 0.45	990.7 \pm 5.07					
	Night	Evening	394	16.74 \pm 5.26	60.01 \pm 12.72	3.45 \pm 1.06	0.18 \pm 1.13	989.76 \pm 5.0					
		Night	395	11.49 \pm 5.98	81.03 \pm 9.74	2.72 \pm 1.22	0.05 \pm 0.27	990.47 \pm 5.17					
Male	Winter	Morning	349	4.66 \pm 4.84	77.24 \pm 10.12	3.43 \pm 1.25	0.04 \pm 0.32	995.83 \pm 5.67					
		Midday	309	12.04 \pm 4.84	51.74 \pm 15.38	4.71 \pm 1.32	0.03 \pm 0.24	994.18 \pm 5.74					
	Night	Evening	339	8.75 \pm 4.83	60.87 \pm 13.44	2.93 \pm 1.0	0.08 \pm 0.38	993.72 \pm 5.58					
		Night	355	4.33 \pm 5.32	78.21 \pm 9.43	2.85 \pm 1.18	0.07 \pm 0.53	994.58 \pm 5.73					

Table 3.4 Differences in mean (\pm SE) movement (m) of females and males on the Samuel Roberts Noble Foundation in southern Oklahoma during 1999-2005 relative to weather conditions. Weather conditions were classified as below normal (i.e., low) if ≤ 1 SD from mean, above normal (i.e., high) if ≥ 1 SD from the mean, and normal if SD was -1 to 1. Values with the same letter did not differ at $\alpha = 0.05$.

Sex	Season	Time period	Variable	F	df	P	Low (≤ -1 SD)	Normal (-1 to 1)	High (≥ 1 SD)
Female	Spring	Midday	Temperature	5.53	2, 116	0.005	935 (143) A	784 (129) AC	568 (140) B
		Evening	Humidity	3.27	2, 194	0.04	774 (136) A	893 (124) AB	999 (132) B
	Summer	Midday	Temperature	4.18	2, 197	0.017	1068 (137) A	846 (126) B	877 (132) AB
		Evening	Humidity	3.88	2, 95.9	0.024	283 (51) A	444 (30) B	359 (64) AB
Male	Spring	Midday	Temperature	3.40	2, 186	0.035	1322 (110) A	1021 (55) B	1160 (118) AB
		Evening	Humidity	3.40	2, 186	0.035	1322 (110) A	1021 (55) B	1160 (118) AB
	Summer	Midday	Temperature	14.33	2, 182	<0.001	1223 (52) A	1200 (52) A	610 (100) B
		Evening	Humidity	14.33	2, 182	<0.001	1223 (52) A	1200 (52) A	610 (100) B
	Spring	Midday	Wind speed	3.45	2, 160	0.034	1330 (104) A	1061 (56) A	942 (113) B
		Evening	Temperature	5.97	2, 248	0.003	1268 (98) A	1070 (70) AB	867 (96) B
	Summer	Midday	Precipitation	6.70	1, 279	0.01	---	519 (50)	844 (133)
		Evening	Temperature	4.21	2, 279	0.016	623 (65) A	476 (53) B	559 (64) AB

Table 3.4 Continued.

Sex	Season	Time period	Variable	<i>F</i>	df	<i>P</i>	Low (≤ -1 SD)	Normal (-1 to 1)	High (≥ 1 SD)
Male	Winter	Evening	Humidity	4.93	2, 244	0.008	1256 (139) A	940 (121) B	987 (140) AB

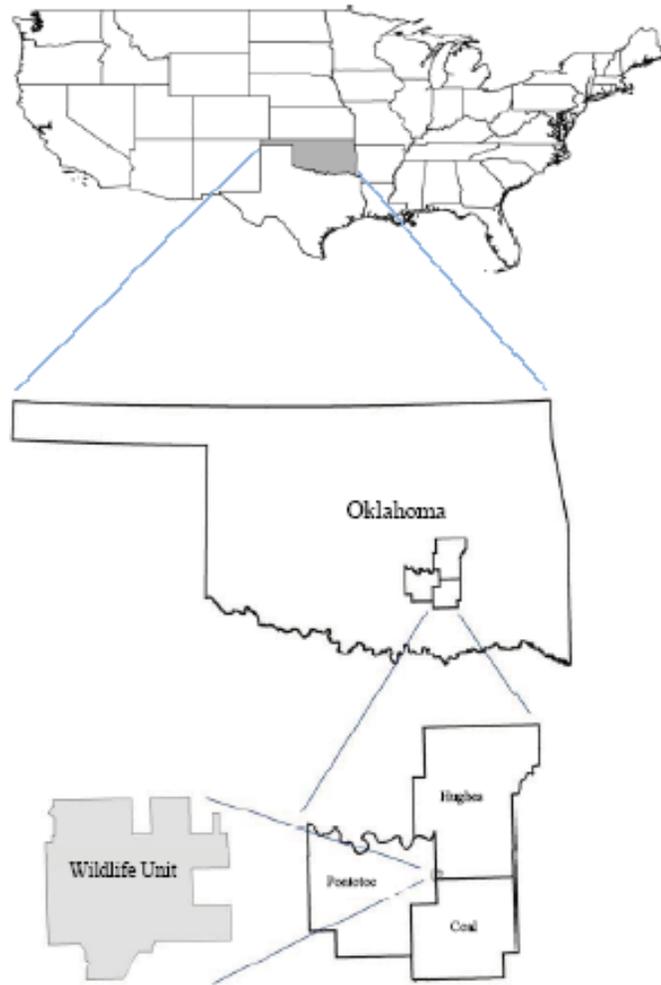
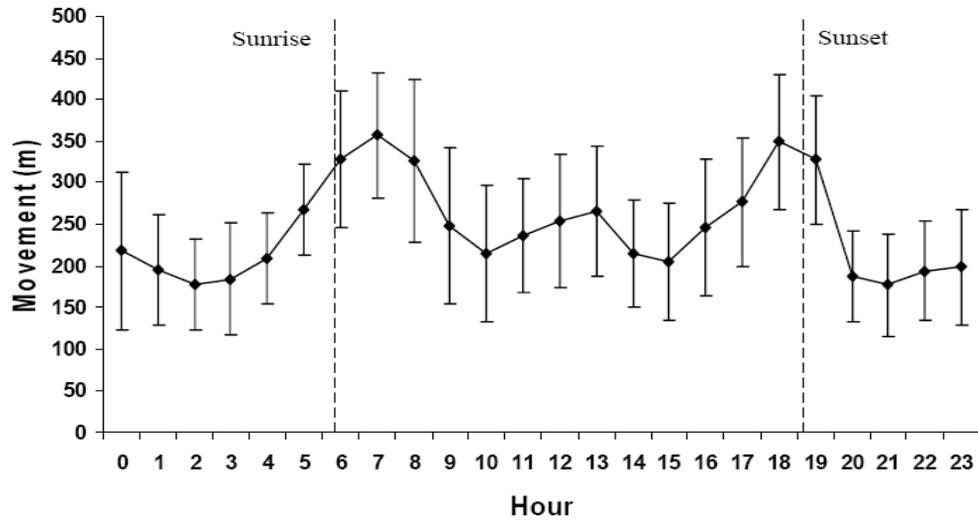


Figure 3.1 Samuel Roberts Noble Foundation Wildlife Unit located in Coal, Hughes, and Pontotoc Counties, Oklahoma, USA.

A)



B)

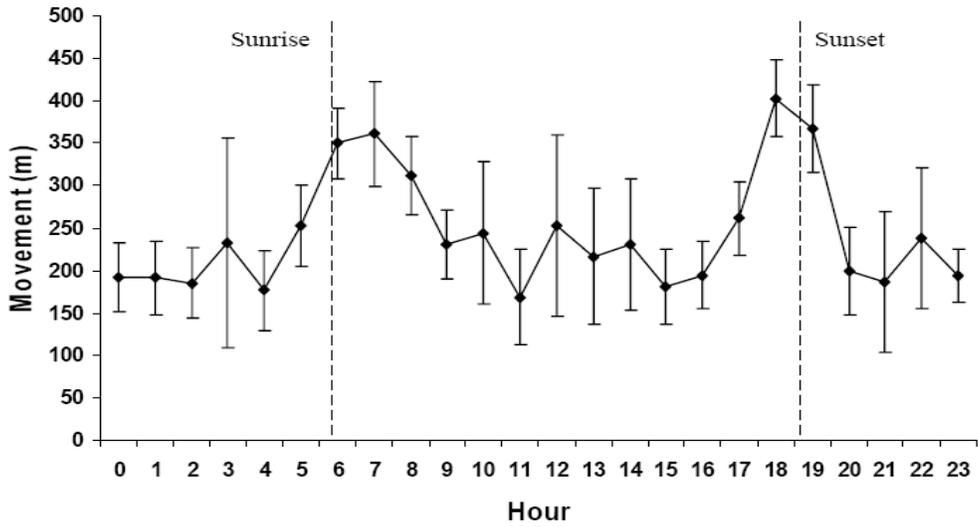
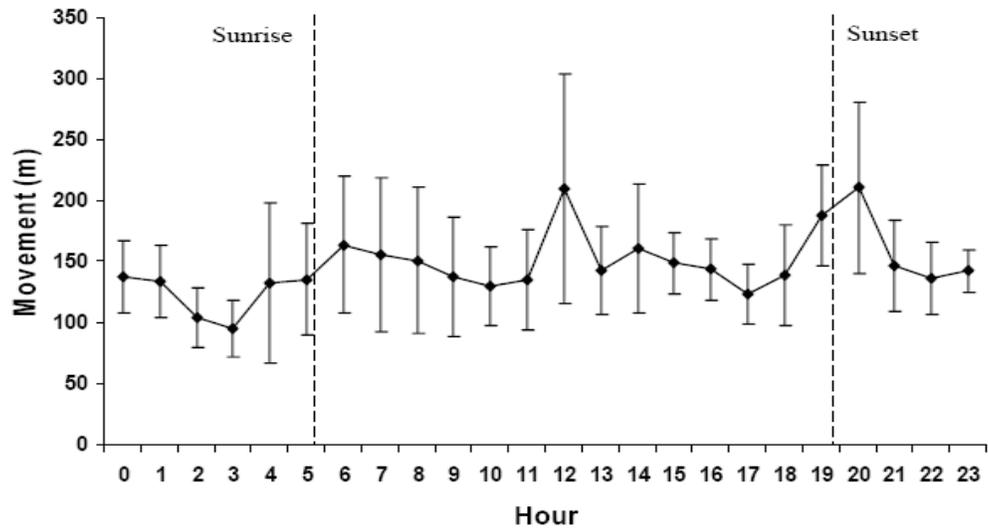


Figure 3.2 Mean hourly movements (m) of female (A) and male (B) white-tailed deer during spring (March-May) on the Samuel Roberts Noble Foundation Wildlife Unit in southern Oklahoma from 1999-2005. Errors bars represent 95% CI around the mean.

A)



B)

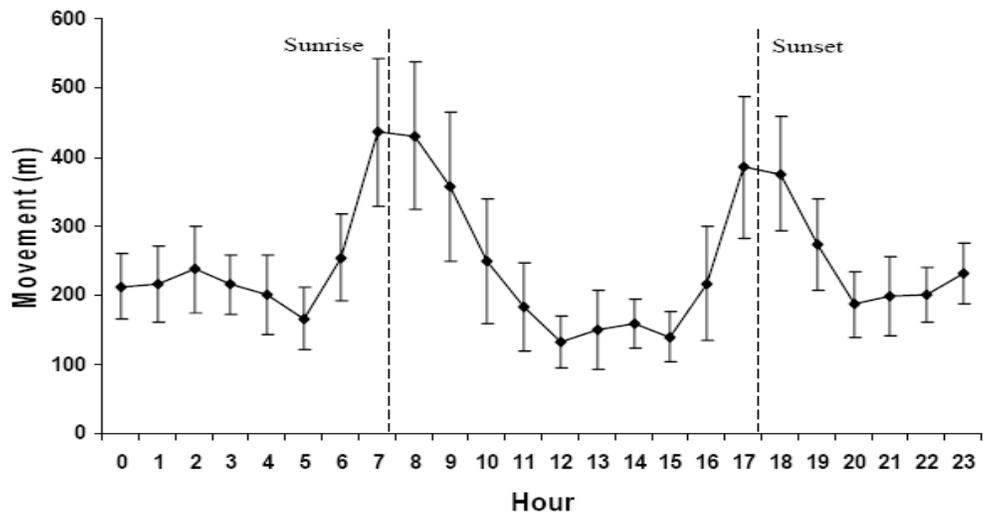


Figure 3.3 Mean hourly movements (m) of female (A) white-tailed deer during summer (June-August) and male (B) white-tailed deer during winter (November-February) on the Samuel Roberts Noble Foundation Wildlife Unit in southern Oklahoma from 1999-2005. Errors bars represent 95% CI around the mean.

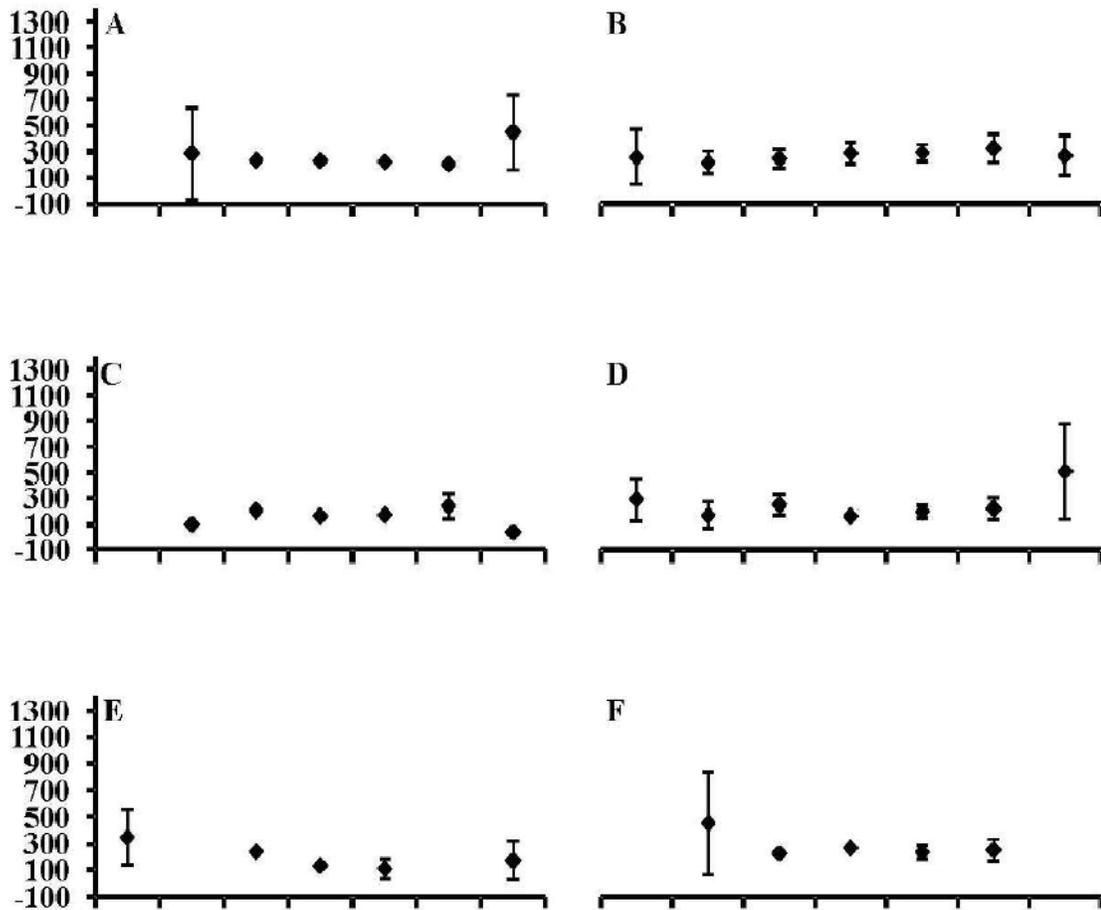


Figure 3.4 Plots of the effects of changes in weather within hour from day to day on hourly deer movements. Temperature influenced movements (m) of females during spring at 0100 hr (A; $F_{5,368} = 2.41$, $P = 0.036$) and males during winter at 1300 hr (B; $F_{6,227} = 4.1$, $P < 0.001$). Male movements were affected by relative humidity during spring at 0100 hr (C; $F_{5,341} = 2.56$, $P = 0.027$) and 1300 hr (D; $F_{6,244} = 3.78$, $P = 0.001$). Precipitation influenced female movements at 1300 hr during summer (E; $F_{6,225} = 3.35$, $P = 0.004$). Pressure affected movements of females during spring at 0100 hr (F; $F_{4,370} = 2.58$, $P = 0.037$) and summer at 0200 hr (G; $F_{2,230} = 3.12$, $P = 0.046$) and male movements during winter at 1300 hr (H; $F_{5,225} = 4.82$, $P < 0.001$). Male movements during winter were affected by wind speed at 1300 hr (I; $F_{6,225} = 3.35$, $P = 0.004$) and 1800 hr (J; $F_{6,303} = 3.01$, $P = 0.007$). Movements on Y-axis.

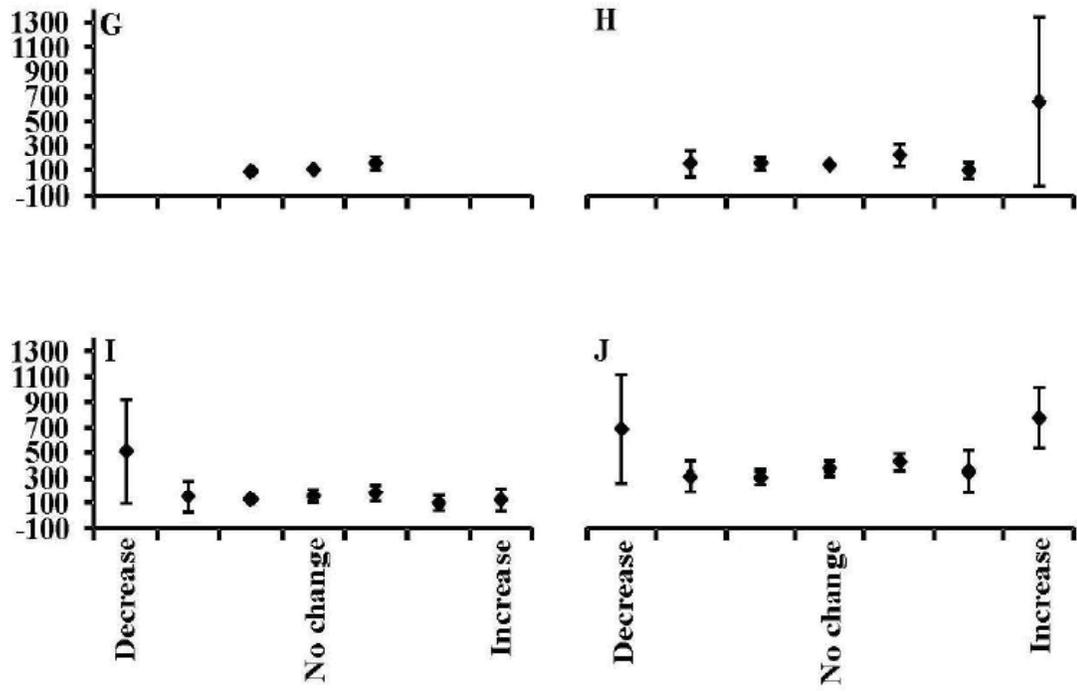


Figure 3.4 Continued.

CHAPTER IV
TESTING A LOCAL INBREEDING HYPOTHESIS AS A CAUSE OF
OBSERVED ANTLER CHARACTERISTICS IN MANAGED
POPULATIONS OF WHITE-TAILED DEER

ABSTRACT

State agencies use antler restrictions (AR) during hunting season to protect young males from harvest and increase prevalence of older male white-tailed deer (*Odocoileus virginianus*). The increased use of AR has led to a focus on antlers by the hunting public, particularly the potential for an association between genetic quality and antler characteristics. I analyzed microsatellite data from 1,231 deer from 3 states to determine if genetic relatedness, internal relatedness (IR), homozygosity weighted by locus (HL), or correlations among uniting gametes (F_{is}) influenced total antler points, antler score, non-typical points or antler malformations. Within each location, deer in the lower and upper quartile intervals for each antler characteristic were unrelated (95% CI included 0 or was <0) and relatively heterozygous with no differences between lower and upper quartiles (95% CI overlapped) for 4 measures of inbreeding. Antler score and points were positively influenced by age but negatively influenced by IR and HL except for antler score in Mississippi. Relatedness, HL, IR and F_{is} did not differ between groups of deer with and without antler malformations. We found 4 of 7 individual deer with malformed

antlers from Oklahoma and 2 of 5 and 3 of 5 individuals from Texas were more homozygous than the average of deer without antler malformations using IR and HL. Perceived differences in antler quality do not appear to be affected by heterozygosity or a result of close inbreeding because I found deer were unrelated and measures of inbreeding and genome-wide heterozygosity were not correlated with antler characteristics in 3 populations of white-tailed deer. These data will aid in decision making processes for managing harvest of white-tailed deer.

INTRODUCTION

In the US, state game agencies play a large role in managing ungulate habitat and population demographics (e.g., age structure and sex ratio) through changes in harvest regulations. Harvest is regulated through season length, bag limits, and restrictions on sex and age classes eligible for harvest. Recently, many states in the southeastern US have adopted antler restrictions (AR; Demarais et al. 2005) to balance male age structure and bring sex ratios closer to unity in white-tailed deer (*Odocoileus virginianus*). The increased use of AR has led to a focus on antlers by the hunting public, particularly the potential for an association between genetic quality and antler characteristics. Antler size is correlated with age (Jacobson 1995, Lukefahr and Jacobson 1998, Strickland and Demarais 2000), where a male's first set of antlers is typically much smaller and the largest antlers are produced by prime-aged males (i.e., 4.5-6.5 years). If carefully constructed, AR shift a typically male-biased harvest from yearling males to older age classes by protecting all males with small antlers based on criteria such as number of

antler points, spread between main beams or a combination of both. For instance, Mississippi shifted the relative composition of males harvested from predominantly 1.5 years (59%) to 2.5 and older (83%) by protecting all males with <4 antler points (Demarais et al. 2005).

Increased emphasis on management and harvest of animals based on antler or horn characteristics has raised concerns over potential biological impacts. Antler regulations in Mississippi reduced antler sizes of cohorts in a variety of soil physiographic regions by differentially protecting smaller-antlered young males and allowing harvest of larger-antlered young males (Demarais et al. 2005). Phenotype-based selective harvest practices for bighorn sheep (*Ovis canadensis*) may have decreased horn size and breeding values for horn size (Coltman et al. 2003). Harris et al. (2002) highlighted genetic consequences of hunting under certain circumstances because the population demographics altered by hunting (e.g., density, sex ratio, and age distribution) influenced population genetics.

In addition, public inquiries expressing concern related to white-tailed deer antler characteristics, particularly antler malformations and possible genetic basis (as a result of inbreeding or high-grading for instance), have increased during the past decade (B. Murphy, Quality Deer Management Association, personal communication). Deer with malformed antlers typically only have 1 side affected, where the length of the main beams and number of antler points is reduced on the affected side. A query of Mississippi's Deer Management Assistance Program (DMAP) database over 12 years identified <0.4% (362 of 10,507) of deer exhibited abnormal antler development, defined

as a $\geq 50\%$ departure in main beam length from the opposite antler (B. K. Strickland, personal communication). Thus, a small percentage of deer are receiving increased attention, perhaps due to an apparent increase in occurrence, as AR result in increased encounter rates of males aged >1.5 years.

Several studies have found a genetic link between heterozygosity of allozymes and morphometric traits in ungulates. Heterozygosity has been used as a measure of recent inbreeding because it is expected to be inversely correlated with inbreeding (Falconer and Mackay 1996, Coltman et al. 1998, Coulson et al. 1998). Deer with small antlers were more inbred, based on heterozygosity of allozymes, than deer with larger antlers (Smith et al. 1976). Individuals which were more heterozygous had greater antler sizes or points in white-tailed deer (Smith et al. 1983, Scribner et al. 1984, Scribner and Smith 1990, Smith et al. 1991) and greater horn growth in bighorn sheep (Fitzsimmons et al. 1995).

Antler traits such as points and mass are heritable (Williams et al. 1994, Lukefahr and Jacobson 1998, Kruuk et al. 2002); thus, there is a genetic component to antler characteristics. Increased relatedness among deer with similar antler characteristics indicates that the antler trait is heritable (Hicks and Rachlow 2006). One solution, to determine whether a genetic link to observed antler characteristics is possible, is to conduct genetic analyses of a group of deer within the population exhibiting unique antler traits (e.g., points and score) that are heritable or rare in occurrence (e.g., antler malformations).

More information is needed by state game agencies for dissemination to the general public on the effects of genetics on antler development and the cause of abnormal antler development. Antler characteristics provide a useful quantitative metric for genetic analysis because much is known about white-tailed deer antlers and their relationships with nutrition, stress, environment and age. Deciduous secondary sexual characters such as antlers demand high levels of nutrition to produce (French et al. 1956, Ullrey 1982, Ditchkoff et al. 2001a). Antlers could be considered a handicap to produce (Zahavi 1975) because only the most-fit males should be able to afford to produce large antlers. Males with smaller antlers or antlers that fluctuate from bilateral symmetry may not be as able to cope with environmental stresses or physical damage (Baccus and Welch 1982). Therefore, antlers may serve as a signal to the genetic quality of the individual during the breeding season (Gould 1974, Ditchkoff et al. 2001a, Ditchkoff et al. 2001b).

I examined the link between antler characteristics and multi-locus heterozygosity as a measure of inbreeding. I used 3 types of antler traits (Hartl and Clark 1997): 1) continuous traits, with a continuous range of values (e.g., antler score), 2) meristic traits, with discrete, integral classes (e.g., antler points), and 3) discrete traits, whether present or absent (e.g., non-typical points) from 3 diverse populations. I used samples from an 8,000 ha free-ranging population, a 1,214 ha enclosed population, and a 3,200 ha free-ranging population managed using AR to test the local inbreeding hypothesis as an explanation for differences in antler points, score, presence of non-typical points and rare occurrences of antler malformations. I focused on 2 levels of classification: 1) the effects of relatedness and inbreeding on groups of individuals with similar antler characteristics

and 2) effects of individual multi-locus heterozygosity on observed antler points and score. My objectives were to determine whether: 1) genetic relatedness and level of heterozygosity among a priori groups of male deer were different based on total antler points, antler score, non-typical points or antler malformations and 2) antler points and score were related to heterozygosity.

STUDY AREA

Mississippi

The Noxubee National Wildlife Refuge (NNWR) was 19,425 ha located in northeastern Mississippi in the counties of Noxubee, Oktibbeha, and Winston, which was in the Interior Flatwoods soil resource region (Pettry 1977). NNWR was comprised of bottomland hardwoods, upland hardwoods, pines, wetlands, and herbaceous vegetation. Public hunting was allowed on ~17,500-ha of the NNWR but sample collection was concentrated on ~3,200 ha. Males and females were harvested at the same intensity; ~1 deer/85 ha. Most harvested males (70-80%) were ≤ 2.5 years-of-age (DeYoung 2004).

Oklahoma

The 1,214-ha Noble Foundation Wildlife Unit (NFWU) was 8.0 km south of Allen, Oklahoma in the Cross Timbers region (Gee et al. 1994). A 2.5 m high-tensile electric fence containing 15 smooth wire strands was erected in 1992 to discourage human trespass and facilitate white-tailed deer management programs (Webb et al.

2009a). The NFWU was approximately 60% wooded and 40% open, with a high degree of interspersed (Gee et al. 1994). Hunting was restricted beginning in 2000 due to ongoing, long-term genetic research projects. Harvest was moderate for females (1 deer/80 ha) and limited for males, most of which were ≥ 2.5 years (~ 1 male/500 ha; DeYoung 2004).

Texas

The Laureles Division of the King Ranch was located 4 km east of Kingsville in Kleberg County, Texas. The 103,691-ha division contained no deer-proof fences. Sampling was conducted on approximately 8,000 ha. The division was characterized as a mixed shrub rangeland dominated by mesquite (*Prosopis glandulosa*) and huisache (*Acacia farnesiana*; McCoy et al. 2005). Females were harvested at ~ 1 female/300 ha and males at ~ 1 male/250 ha (M. W. Hellickson, King Ranch Inc., personal communication).

METHODS

Sample collection

Mississippi

In Mississippi, deer on NNWR were sampled by harvest or special collection by the Mississippi Department of Wildlife, Fisheries, and Parks (MDWFP) or NNWR

personnel from 1999-2001. Muscle or tissue samples were collected from all harvested deer because check-in of harvested deer was mandatory. During spring special collections, adult females were collected as part of the MDWFP's population health assessment monitoring program. Fetuses obtained from females provided known dam/offspring relationships. Muscle and tissue samples were frozen and stored at -20°C . I used predictive equations described by Strickland and Demarais (2000) to calculate gross Boone & Crockett score (hereafter score; Boone and Crockett Club 1997) from available antler measurements (i.e., number of antler points, inside spread, main beam lengths, and basal circumferences). Score is a means of assessing total antler grown and is a composite index to antler length and mass. In 1995, Mississippi initiated a statewide AR only allowing the harvest of males with ≥ 4 antler points (Demarais et al. 2005). There was the potential that males harvested in Mississippi were not a random sample due to the imposed AR, whereas capture of deer in Oklahoma and Texas allowed for a more representative sample of deer on the study area.

Oklahoma

Deer were captured using a drop-net (Ramsey 1968, Gee et al. 1999) baited with corn from January-April 1991-2005. I sedated deer using Xylazine (3-6 mg/kg, Phoenix Scientific, St. Joseph, Missouri, USA) or a Telazol[®]-Xylazine mixture (4.4 mg/kg Telazol, [®] Fort Dodge Animal Health, Fort Dodge, Iowa, USA, plus 2.2 mg/kg xylazine) and used yohimbine (Abbott Laboratories, North Chicago, Illinois, USA) at 0.125 mg/kg or tolazine (Lloyd Laboratories, Shenandoah, Iowa) at 0.4 mg/kg as an antagonist to the

xylazine. Blood (20ml/deer) was obtained from captured deer and preserved in 0.5M EDTA and stored at 4°C. Tissue samples were taken from all harvested deer that had not previously been captured, and samples were stored at -20°C. Fetuses were collected from harvested does to provide known dam/offspring relationships. Shed antlers also provided additional DNA samples from males not harvested or captured. Antlers were measured and scored according to Boone and Crockett scoring standards (Boone and Crockett 1997). However, I excluded inside spread from the final score because antlers were removed from deer at time of capture and later scored; therefore, I could not determine inside spread.

Texas

Deer were captured using a helicopter and net-gun (Webb et al. 2008) and collected a tissue sample via ear punch during September-October from 1999-2005. Muscle samples were also collected on all harvested deer along with fetuses of harvested females, also providing known dam/offspring relationships. Tissue samples were frozen and stored at -20°C until DNA could be extracted. Antlers were measured and scored at time of capture or harvest according to Boone and Crockett scoring standards (Boone and Crockett 1997).

DNA isolation and extraction

DNA was isolated from whole blood as described by DeYoung et al. (2003). Tissue samples were sectioned (~0.5 cm³) and scored with a razor blade to increase

surface area. I isolated DNA using Qiagen® DNeasy® tissue kits (Qiagen® Genomics Inc., Bothell, Washington, USA). Supplier recommendations were followed except that tissue lysis was performed with 30µl Proteinase K (20 mg/ml) with overnight incubation. DNA was also extracted from bones and antlers from the NFWU as described by DeYoung (2004).

DNA amplification and separation

I used 17 microsatellite markers (INRA011, Cervid1, ILSTS011, BovPRL, N, Q, K, BL25, BM6438, O, BM848, R, BM6506, P, BM4208, OarFCB, and D) evaluated by DeYoung et al. (2003) from a 21 locus cervid microsatellite panel (Anderson et al. 2002). Deer with <10 scored loci were excluded from analyses. Extracted DNA was amplified via polymerase chain reaction (PCR) on a PE Gene Amp® 9600 thermocycler (Applied Biosystems Inc., Foster City, California, USA) using fluorescent tagged primers in single and multiplexed reactions. For a complete description of reaction conditions and primers see Anderson et al. (2002). PCR products were mixed together from 2-4 reactions (~3 µl from each reaction) and 1 µl of this mixture was applied to a denaturing formamide and size standard mix (GeneScan™ 500 ROX™; Applied Biosystems Inc.). PCR product and denatured mixes were loaded onto an ABI Prism® 3130 Genetic Analyzer (Applied Biosystems Inc.) for separation and detection. DNA was analyzed and alleles assigned using GeneMapper® software (Applied Biosystems Inc.).

Data analysis

Antler groups

I assigned deer to a priori antler groups based on similar antler characteristics to determine whether deer with similar antlers shared common ancestors or showed similar levels of heterozygosity. I determined study area and age-specific quartiles (i.e., lower and upper 25%) for antler points and score (Table 4.1). Deer with the largest antlers (i.e., number of points and score) in the upper 25% quartile and deer with the smallest antlers in the lower 25% quartile were compared. Deer were also placed into 1 of 2 groups based on presence or absence of non-typical points because a smaller proportion of the population grows these extra points. Deer were further classified into groups with no non-typical points and deer with ≥ 2 non-typical points. Each male deer only entered the dataset once even if multiple years of data were available. If multiple years of data were available, I classified deer based on the number of years with the most frequent non-typical classification. For example, I classified a deer with 1 year of no non-typical points, 1 year of 1 non-typical point, and 2 years with ≥ 2 non-typical points as a deer with ≥ 2 non-typical points. Last, deer were grouped depending on whether they exhibited normal or malformed antlers. Malformed antlers were classified based on a $>50\%$ departure in main beam length between the left and right antlers or a departure of $>60\%$ between number of antler points on each antler. I used data from Oklahoma and Texas because data on antler points from Mississippi was unavailable and no deer exhibited $>50\%$ departure between left and right main beams. Similar to designations by

Rachlow et al. (2003), I classified deer with normal antlers as those deer with antlers that conformed to the shape and orientation representative of the species (Boone and Crocket Club 1997). Deer with malformed antlers typically had 1 malformed antler, were smaller than the corresponding normal antler, and contained fewer antler points.

Age estimation

Deer age was estimated using tooth replacement and wear techniques (Severinghaus 1949) on all 3 study areas. Deer that were not of known-age at time of harvest or capture (i.e., fawn or yearling) were conservatively placed into age class (Gee et al. 2002). I analyzed data for 1, 2 and 3 year-old males due to limited sample sizes for deer ≥ 4 years of age for antler point and score analyses. I used all ages for documenting relatedness of the sexes and for group comparisons of typical versus non-typical antler points.

Relatedness

I calculated genetic relatedness (r) as a means of detecting the presence of close relationships among groups of deer with similar antler characteristics. I used Queller and Goodnight's (1989) regression method to estimate relatedness. The relatedness estimator uses population allele frequencies to estimate the proportion of alleles between 2 individuals that are identical by descent. Variability of r estimates is due to weighting of r by the frequency of shared alleles with rare shared alleles being weighted more heavily than shared common alleles (Queller and Goodnight 1989).

Pairwise comparisons of r among deer were restricted to within antler characteristic and group. When group comparisons were conducted, I used allele frequencies from the whole sample as the reference population. Mean r and 95% confidence intervals were computed by jackknifing over loci and compared between groups within antler characteristic. I used Spatial Pattern Analysis of Genetic Diversity (SPAGeDi) 1.2 (Hardy and Vekemans 2002) for calculating r .

Internal relatedness

I calculated internal relatedness (IR) as a measure of heterozygosity. Internal relatedness, similar to Queller and Goodnight's (1989) measure of relatedness between individuals or groups, is a measure based on allele sharing where the frequency of each allele counts towards the final score where shared rare alleles are weighted more than common alleles (Amos et al. 2001). Internal relatedness values are approximately normally distributed and centered around mean zero (Amos et al. 2001), similar to relatedness values. Values near zero suggest individuals were born to unrelated parents while negative values indicate higher heterozygosity and positive values suggest higher homozygosity or inbreeding (Amos et al. 2001). I calculated IR using a macro (IRmacroN4) written in Visual Basic code for Microsoft Excel (<http://www.zoo.cam.ac.uk/zoostaff/amos/#ComputerPrograms>; accessed 27 August 2008).

Homozygosity weighted by locus

I calculated homozygosity weighted by locus (HL) using IRmacroN4.

Homozygosity is estimated by weighing the contribution of each locus to the index score rather than the contribution of each allele, which gives more weight to more informative loci (i.e., more alleles/locus and more evenly frequent; Aparicio et al. 2006). This is important when few microsatellite markers are used and when the markers differ in allelic diversities (Aparicio et al. 2006). This measure varies between 0 and 1; 0 when all loci are heterozygous and 1 when all loci are homozygous.

F-statistics

Last, I calculated F -statistics (Wright 1951) as a way to describe genetic population structure in diploid organisms. F_{is} was defined by Wright (1951) as the correlation between homologous alleles within samples with reference to the local population. I used Weir and Cockerham's (1984) method of calculating F_{is} in SPAGeDi because their method weights F_{is} from each sample by its sample size to take into account unequal sample sizes. More homozygous individuals will be positive (maximum = 1) indicating positive correlations among uniting gametes due to inbreeding whereas more heterozygous individuals will be negative (minimum = -1) under Hardy-Weinberg equilibrium (HWE; Avise 2004).

Sex and sibling pair analysis

I calculated sex-specific estimates of r as a reference of the underlying r of each of the 3 study populations. Group r was estimated for females and males separately and then together. I plotted sex- and population-specific multilocus pairwise genetic coefficients (i.e., r) for later use in qualitative comparisons with antler group distributions. For plotting purposes, I divided r into 20 equidistant segments in units of 0.1 from -1 to 1 .

Each year, on the 3 study areas, females were harvested and fetuses collected and genotyped, which provided known sibling pairs. I estimated an average within group (i.e., fetuses within dam) r of sibling pairs. Theoretically, expected r of full siblings should be 0.5 and 0.25 for half siblings, which may result from multiple paternities (DeYoung et al. 2002, Sorin 2004). Distributions of pairwise r estimates were also plotted for reference.

Antler analyses

I calculated study area and age-specific means and corresponding 95% CI for r , IR, HL, and F_{is} for each antler characteristic (i.e., antler points, score, non-typical antler points and antler malformations) to determine whether there was a difference between antler groups (i.e., lower and upper quartiles and presence or absence of non-typical points and antler malformations). I tested the relationship between antler points and score (dependent variables) and IR and HL (explanatory variables) using general linear mixed models (GLMM; PROC MIXED; SAS Institute 2003) with deer identification,

year and study area as random effects. Using deer identification as a random effect enabled me to account for pseudoreplication of measurements taken on the same individuals in different years. Year and study area were modeled as a random effects, which took into consideration random environmental variation from year to year and from study area to study area. Age was included as a covariate to control for differences in age-specific antler size. I examined plots of residuals and normal probability plots to ascertain whether data were normally distributed. I conducted all statistical analyses using SAS 9.2 (SAS Institute 2003). I concluded statistical significance for $P \leq 0.05$. For all GLMM I used a degrees of freedom adjustment developed by Kenward and Roger (1997). The Kenward-Roger option accounts for unbalanced data, multiple random effects, and any model with correlated errors (Littell et al. 2006).

RESULTS

I genotyped 1,231 deer; 259 from Mississippi, 529 from Oklahoma, and 443 from Texas. Previous research from the same study populations revealed no significant linkage disequilibrium or deviations from HWE (DeYoung et al. 2009).

Relatedness

Females and males, and both sexes combined, on all 3 study areas had mean r near zero (i.e., 95% CI included zero or was < 0 ; Table 4.2) indicating deer were unrelated. Distributions of pairwise r estimates were normally distributed around $\bar{x} = 0$ for females and males on all 3 study areas (Figure 4.1a-c). No more than 7.4% of

pairwise relatedness estimates exceeded 0.25 for any sex in any population (range: 3.9-7.4%).

I detected higher levels of r by using known sibling pairs from all 3 study areas. Mean r was 0.415 (0.024), 0.405 (0.04), and 0.439 (0.022) for sibling pairs in Mississippi, Oklahoma, and Texas, respectively (Table 4.2), which is between the theoretical values of half siblings (0.25) and full siblings (0.50). The majority of sibling pairs in Mississippi were related between 0.25 and 0.5 with $r = 0.5$ having the highest frequency (Figure 4.2). In Oklahoma, the highest frequency of pairwise comparisons occurred around 0.4 (25%) followed by 0.2 (15%), 0.3 (15%) and 0.5 (15%; Figure 4.2). Fifty seven percent and 23% of siblings were related around 0.5 and 0.25, respectively in Texas (Figure 4.2). In Mississippi, Oklahoma, and Texas only 6%, 5%, and 2% of pairs were estimated to be unrelated (Figure 4.2).

All antler groupings (i.e., antler points and score, non-typical points and antler malformations) were unrelated regardless of age or study area because 95% CI included zero or were < 0 (Table 4.3). Confidence intervals of all antler group comparisons overlapped; therefore, there was no difference between antler groups (Table 4.3). I compared distributions of antler groupings (i.e., antler points and score and non-typical points) to known sibling pair distributions and sex-specific distributions as a reference. Distributions of pairwise r were normally distributed around $\bar{x} = 0$ and did not show bimodal or skewed distributions.

Internal relatedness

Mean IR of all males was 0.034 (0.015 SE), 0.056 (0.013 SE), and 0.087 (0.013 SE) for Mississippi, Oklahoma and Texas populations, respectively. Mean IR of antler groups ranged from 0.003-0.131. Most (29 of 44; 66%) antler group IR scores indicated deer within antler group were unrelated because 95% CI included zero (Table 4.3). The remaining 15 antler groups tended to be slightly more homozygous because 95% CI were > 0 (Table 4.3). However, IR did not differ between groups of deer with the most and fewest points, highest and lowest scores, and the presence and absence of non-typical points and antler malformations, as revealed by comparisons of 95% CI (Table 4.3).

Generalized linear mixed models revealed no effect of IR on antler points ($F_{1,354} = 2.56, P = 0.11$) or score ($F_{1,343} = 2.36, P = 0.126$). However, I did observe a qualitative negative trend between IR and antler points and score; as IR increased antler points and score decreased. Internal relatedness scores of deer from Oklahoma ($n = 7$) and Texas ($n = 5$) with antler malformations were below (3), above (6) and within (3) the 95% CI of IR scores for deer with normal antlers from their corresponding population (Table 4.4).

Homozygosity weighted by locus

Mean HL for all males in Mississippi, Oklahoma and Texas populations were 0.26 (0.012 SE), 0.298 (0.01 SE) and 0.294 (0.009 SE), respectively. Homozygosity estimates for all group comparisons ranged from 0.23-0.349 (Table 4.3). Subtracting HL from 1 gives an estimate of heterozygosity. Therefore, population and antler group heterozygosity ranged from 0.702-0.74 and 0.651-0.77, respectively. Thus, it appears as

though all populations and groups of deer were relatively heterozygous. Additionally, there was no difference between groups of deer with the most and fewest points, highest and lowest scores, and the presence and absence of non-typical points and antler malformations (Table 4.3).

Similar to IR, HL negatively influenced antler points ($F_{1,357} = 4.64$, $P = 0.032$) and score ($F_{1,344} = 3.57$, $P = 0.06$); both decreased with increasing homozygosity. Homozygosity scores of deer from Oklahoma ($n = 7$) and Texas ($n = 5$) with antler malformations were below (4), above (7) and within (1) the 95% CI of IR scores for deer with normal antlers from their corresponding population (Table 4.4).

F-statistics

F_{is} was used to indicate a heterozygote deficit and values ranged from 0.019-0.204 across all antler groups. There was a positive correlation between homologous alleles (i.e., more homozygous or heterozygote deficit) as indicated by positive F_{is} values (95% CI >0) in 11 of 44 groups (25%; Table 4.3). Groups of deer with fewer antler points and lower antler scores (4 of 18) tended to be more homozygous due to inbreeding as well as deer without malformed antlers (Table 4.3). Other groups of deer that tended to be more homozygous included 2 year-old deer with larger antler scores from Texas and groups with and without non-typical points from Oklahoma and Texas (Table 4.3). Despite 11 groups being more homozygous than expected, their 95% CI overlapped with the corresponding antler group comparison (Table 4.3). Therefore, inbreeding, as

indicated by positive F_{is} values, may not strongly be associated with observed differences in antler characteristics.

DISCUSSION

Most deer on all 3 study areas were unrelated and relatively heterozygous. I detected relationships at the full or half sibling level (i.e., 0.5 and 0.25, respectively) from known sibling pairs. Therefore, if any a priori antler groupings were being affected by level of r it is likely I would have been able to detect it at the half sibling level. All 3 measures of heterozygosity (i.e., IR, HL, and F_{is}) revealed deer, regardless of antler group, were relatively heterozygous. Studies of red deer (Coulson et al. 1998) and elk (Hicks and Rachlow 2006) also revealed that deer were relatively heterozygous and close inbreeding rare. However, it is not always inbreeding that would be detected using individual heterozygosity indices because inbreeding is expected to be rare in most populations, especially if polygyny is weak (Balloux et al. 2004) and correlations between individual heterozygosity and inbreeding low (Balloux et al. 2004, Slate et al. 2004). In addition, tests of heterozygosity may reveal heterozygosity effects through linkage with areas experiencing selection (Balloux et al. 2004). For example, von Hardenberg et al. (2007) acknowledged that heterozygosity-fitness correlations for horn growth in Alpine ibex may have been due to linkage disequilibrium and not inbreeding. However, I did not test for linkage disequilibrium by assessing single-locus effects.

There could however be some individuals that did have higher levels of inbreeding in my study. For example, the incidence of antler malformations could reflect

rare cases of close inbreeding because the number of cases was relatively low. For example, severe inbreeding may have led to increased fluctuating asymmetry (i.e., antler malformations) of sika deer (*Cervus nippon*) antlers from a small (39 ha) enclosed population, which was started from 6 founding individuals (Baccus and Welch 1982). As a group, deer with antler malformations in my study were not more related or inbred than the group of deer with normal antlers. These findings are similar to Hicks and Rachlow (2006), which found that elk with malformed antlers were not more related or inbred than elk with normal antlers. These data corroborate that there is minimal evidence for a strong genetic basis of inheritance of antler malformations in randomly mating populations (Hicks and Rachlow 2006).

Environmental or other factors likely played a role in observed antler size and malformations in white-tailed deer. Maternal effects (e.g., non-heritable facets of condition, environment, year, and behavior) are more prominent in 1.5 year old males and to a lesser extent in 2.5 year old males (Lukefahr and Jacobson 1998). I found 3 of 12 and 4 of 12 individuals with antler malformations were 1.5 and 2.5 years of age, respectively. Therefore, antler configuration may have been more related to maternal or environmental factors and not heritable genetic effects. The remaining 5 deer were older, and thus could have sustained a body or pedicle injury predisposing them to developing malformed antlers. Rachlow et al. (2003) found that malformed antlers, in every case, were associated with pedicles deformed in size or orientation. Observations of deer with antler malformations from Mississippi, not included in my study, may also have been due to pedicle deformation or injury (S. L. Webb, personal observation). I was unable to

determine whether malformed antlers from Oklahoma and Texas were due to deformed pedicles or body injury because deer were classified as malformed from antler measurements, photographs and removed antler sets.

It has long been recognized that age influences antler size (Jacobson 1995, Lukefahr and Jacobson 1998, Strickland and Demarais 2000). Genetic factors, such as heterozygosity or inbreeding, may also contribute to antler size (Scribner et al. 1989, Lukefahr and Jacobson 1998). When testing for effects of heterozygosity on antler size, I accounted for age-specific antler size. There was not a strong linear relationship between IR and individual antler points or score, although a qualitative negative trend was observed. However, HL was more strongly related to both antler measures and revealed the same negative trend. Therefore, HL explained more variation in individual antler size than IR. My findings are similar to previous research which found a genetic link between heterozygosity of allozymes and morphometric traits in ungulates. Deer with small antlers were more inbred, based on heterozygosity of allozymes, than deer with larger antlers (Smith et al. 1976). Individuals which were more heterozygous had greater antler sizes or points in white-tailed deer (Smith et al. 1983, Scribner et al. 1984, Scribner and Smith 1990, Smith et al. 1991) and greater horn growth in bighorn sheep (Fitzsimmons et al. 1995).

In my study, antler size may not be an honest signal of genetic quality (i.e., increased heterozygosity) because most heterozygosity-antler size relationships were weak when based on neutral markers. In addition, parameter estimates were small indicating minor changes in antler size with increasing homozygosity. Therefore, loci

linked to immunogenetic regions (Acevedo-Whitehouse et al. 2005, von Hardenberg et al. 2007) or variation of loci at the major histocompatibility complex (Ditchkoff et al. 2001b) may reveal more information about the genetic quality of the individual.

Factors such as hunting (Hartl et al. 1995, Harris et al. 2002, Hartl et al. 2003), population size (Ryman et al. 1981), and confinement to fenced enclosures (Hartl et al. 2003) may affect genetic characteristics of the population. Increased homozygosity (i.e., inbreeding) may occur when populations are relatively small and isolated (Coltman et al. 1998, Zachos et al. 2007). Therefore, my enclosed population (i.e., NFWU) may have showed signs of increased inbreeding due to reduced gene flow or mating between close relatives. However, the enclosed population showed similar levels of heterozygosity to large free-ranging populations from Mississippi and Texas for several reasons. First, the HTEF surrounding the Oklahoma property was not a complete barrier to deer movements (Webb et al. 2009a, b). Second, GPS collar data (Webb et al. 2009a) revealed deer could enter the study area and mitochondrial DNA data (R. Toby, unpublished data) revealed deer were actually entering the study area. Last, the HTEF surrounds a relatively large area, has not been up long in terms of deer generations, and encloses a population of deer consisting of several hundred individuals (K. L. Gee, Samuel Roberts Noble Foundation, unpublished data). Despite the HTEF, the study area was allowing enough immigration to avoid serious genetic problems.

Selective harvest has also been implicated in influencing genetic properties of hunted populations (Ryman et al. 1981, Hartl et al. 1995, Harris et al. 2002, Coltman et al. 2003, Hartl et al. 2003). Horn size of bighorn sheep rams decreased due to intense

harvest pressure of rams with large horns (Coltman et al. 2003). In Mississippi, a 4-point AR resulted in a shift to fewer antler points of deer at 3.5 years of age (Demarais et al. 2005). If antler quality were related to genetic variability (i.e., heterozygosity), and selective harvest influences genetic variability, then I might expect heterozygosity to differ between Mississippi and my 2 other populations. Based on these data, all populations had similar levels of neutral genetic diversity. Therefore, AR may not result in changes in population level genetic diversity because antler size and heterozygosity were not strongly related. Other factors, such as environment, may exert a greater influence on antler morphology (Kruuk et al. 2002). In addition, antlers may not be the true object of selection (Kruuk et al. 2002), which would result in no change of genetic diversity from selective harvest.

The ability to detect inbreeding from a modest number of microsatellite loci is limited, but based on these data there was no detectable difference in breeding. Therefore, deer were unlikely to suffer from inbreeding (i.e., increased r and homozygosity) or reduced genetic diversity under the conditions described here and in DeYoung et al. (2009). My 2 free-ranging populations were large and allowed movement of individuals into and out of the population. Successful reproduction of dispersing individuals will result in populations of deer being less subdivided genetically. Even my enclosed population was not a complete barrier to deer movement (Webb et al. 2009a, b) and allowed for gene flow among populations. Selective harvest programs, under the inbreeding hypothesis, will likely not have an effect on reducing future genetic diversity, particularly if these traits are influenced by other factors such as injury,

nutritional deficiencies, or environmental conditions. There does not appear to be a strong inherited genetic basis for the occurrence of similar antler traits within groups (Hicks and Rachlow 2006) because deer were not inbred and deer with similar antler traits did not share common ancestors. Therefore, selective harvest programs should focus on removing individuals to maintain proper densities and age structures, which may improve mean cohort antler size at maturity, and not to change the genetics of the population.

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Table 4.1 Age-specific lower and upper antler point and score (cm) quartiles used in antler group comparisons from Mississippi (1999-2001), Oklahoma (1991-2005) and Texas (1999-2005).

Metric	Age	Mississippi ¹		Oklahoma ²		Texas ³	
		Lower	Upper	Lower	Upper	Lower	Upper
Score	1	≤104.1	≥137.2	≤78.7	≥142.2	≤76.2	≥137.2
	2	≤188.0	≥233.7	≤167.6	≥256.5	≤180.3	≥238.8
	3	≤195.6	≥292.1	≤236.2	≥281.9	≤254.0	≥309.9
Points	1	≤4	≥6	≤3	≥8	≤2	≥6
	2	≤5	≥8	≤7	≥9	≤6	≥9
	3	≤6	≥8	≤8	≥10	≤7	≥10

¹Predictive equation used to calculate antler score (Strickland and Demarais 2000)

²Inside spread was excluded from final antler score

³Antler score followed Boone and Crockett Club guidelines (Boone and Crockett 1997)

Table 4.2 Relatedness (r) of females, males, sibling pairs, and both sexes combined from Mississippi (1999-2001), Oklahoma (1991-2005) and Texas (1999-2005).

Study area	Group	N	Mean (SE)	95% CI	
				Lower	Upper
Mississippi	Both	197	-0.005 (0.001)	-0.007	-0.003
	Female	53	0.005 (0.008)	-0.012	0.022
	Male	144	-0.008 (0.004)	-0.011	0.022
	Siblings	62	0.415 (0.024)	0.367	0.463
Oklahoma	Both	495	-0.002 (0.003)	-0.007	0.003
	Female	266	-0.003 (0.002)	-0.008	0.002
	Male	229	-0.001 (0.006)	-0.012	0.01
	Siblings	34	0.405 (0.04)	0.324	0.486
Texas	Both	330	-0.006 (0.003)	-0.011	0.000
	Female	132	0.013 (0.011)	-0.008	0.034
	Male	198	-0.012 (0.007)	-0.026	0.002
	Siblings	113	0.439 (0.022)	0.395	0.483

Table 4.3 Relatedness (r), internal relatedness (IR), homozygosity weighted by locus (HL), and F_{is} among male white-tailed deer within age class for lower and upper antler point and score (cm) quartiles and presence (≥ 2) or absence of non-typical points and antler malformations from Mississippi (1999-2001), Oklahoma (1991-2005) and Texas (1999-2005).

Study area	Age	Trait	Class	N	Relatedness		Internal relatedness		Homozygosity		F_{is}	
					Mean (95% CI)	Mean (95% CI)	Mean (95% CI)	Mean (95% CI)	Mean (95% CI)	Mean (95% CI)		
Mississippi	1	Score	Lower	10	-0.013 (-0.098, 0.072)	0.064 (-0.03, 0.158)	0.299 (0.224, 0.374)	0.062 (-0.056, 0.18)				
			Upper	11	-0.055 (-0.087, -0.022)	0.059 (-0.027, 0.145)	0.286 (0.214, 0.358)	0.073 (-0.043, 0.189)				
	Point	Lower	22	-0.022 (-0.050, 0.006)	0.02 (-0.07, 0.111)	0.25 (0.182, 0.319)	0.034 (-0.041, 0.109)					
		Upper	11	-0.04 (-0.077, -0.002)	0.069 (-0.025, 0.164)	0.288 (0.209, 0.366)	0.068 (-0.023, 0.159)					
	2	Score	Lower	8	-0.048 (-0.106, 0.010)	0.031 (-0.104, 0.166)	0.27 (0.165, 0.376)	0.054 (-0.071, 0.17)				
			Upper	9	-0.063 (-0.101, -0.025)	0.105 (0.014, 0.196)	0.303 (0.219, 0.386)	0.115 (-0.003, 0.233)				
Oklahoma	Point	Lower	6	-0.038 (-0.098, 0.021)	0.099 (-0.066, 0.264)	0.308 (0.157, 0.458)	0.103 (-0.08, 0.286)					
		Upper	12	-0.054 (-0.095, -0.013)	0.016 (-0.046, 0.078)	0.23 (0.186, 0.274)	0.024 (-0.046, 0.094)					
	3	Score	Lower	8	-0.04 (-0.086, 0.007)	0.014 (-0.116, 0.145)	0.249 (0.143, 0.355)	0.025 (-0.072, 0.122)				
			Upper	8	0.001 (-0.110, 0.113)	0.017 (-0.109, 0.144)	0.259 (0.164, 0.354)	0.02 (-0.103, 0.143)				
	Point	Lower	12	-0.04 (-0.118, 0.038)	0.026 (-0.066, 0.118)	0.266 (0.195, 0.337)	0.04 (-0.028, 0.108)					

Table 4.3 Continued.

Study area	Age	Trait	Class	N	Relatedness		Internal relatedness		Homozygosity		F_{is} Mean (95% CI)
					Mean (95% CI)	Mean (95% CI)	Mean (95% CI)	Mean (95% CI)			
Mississippi	3	Point	Upper	13	-0.047 (-0.071, -0.023)	0.007 (-0.092, 0.106)	0.242 (0.168, 0.315)	0.02 (-0.072, 0.112)			
	1	Score	Lower	15	-0.007 (-0.033, 0.019)	0.106 (0.023, 0.189)	0.341 (0.276, 0.407)	0.102 (-0.02, 0.224)			
Oklahoma			Upper	15	-0.027 (-0.070, 0.017)	0.01 (-0.083, 0.103)	0.256 (0.188, 0.324)	0.023 (-0.043, 0.089)			
		Point	Lower	19	-0.006 (-0.036, 0.024)	0.112 (0.042, 0.182)	0.349 (0.29, 0.409)	0.113 (0.014, 0.212)			
			Upper	15	-0.013 (-0.048, 0.021)	0.022 (-0.076, 0.12)	0.263 (0.194, 0.331)	0.019 (-0.078, 0.116)			
	2	Score	Lower	11	-0.068 (-0.115, -0.020)	0.059 (-0.031, 0.149)	0.315 (0.248, 0.382)	0.071 (-0.076, 0.218)			
			Upper	12	-0.003 (-0.056, 0.050)	0.032 (-0.076, 0.141)	0.274 (0.186, 0.361)	0.029 (-0.061, 0.119)			
		Point	Lower	15	-0.048 (-0.074, -0.022)	0.122 (0.052, 0.192)	0.345 (0.299, 0.392)	0.129 (0.024, 0.234)			
			Upper	17	-0.03 (-0.063, 0.011)	0.019 (-0.065, 0.104)	0.262 (0.193, 0.331)	0.034 (-0.038, 0.106)			
3		Score	Lower	8	-0.027 (-0.067, 0.012)	0.069 (-0.047, 0.184)	0.311 (0.229, 0.392)	0.073 (-0.045, 0.191)			
			Upper	8	-0.04 (-0.096, 0.015)	0.027 (-0.107, 0.161)	0.271 (0.159, 0.382)	0.042 (-0.072, 0.156)			
		Point	Lower	16	-0.03 (-0.058, -0.003)	0.057 (-0.007, 0.12)	0.304 (0.253, 0.355)	0.064 (-0.015, 0.143)			

Table 4.3 Continued.

Study area	Age	Trait	Class	N	Relatedness		Internal relatedness		Homozygosity		F_{is}
					Mean (95% CI)	Mean (95% CI)	Mean (95% CI)	Mean (95% CI)			
Oklahoma	3	Point	Upper	10	-0.045 (-0.084, -0.005)	0.057 (-0.056, 0.17)	0.296 (0.198, 0.393)	0.067 (-0.057, 0.191)			
	N/A	NT ¹	Absent	81	-0.01 (-0.028, 0.009)	0.08 (0.048, 0.112)	0.31 (0.286, 0.334)	0.086 (0.034, 0.138)			
		Abn ²	Present	19	0.006 (-0.035, 0.047)	0.083 (0.009, 0.156)	0.308 (0.245, 0.37)	0.072 (0.011, 0.133)			
		Score	Yes	7	-0.025 (-0.111, 0.060)	0.119 (0.029, 0.209)	0.329 (0.251, 0.406)	0.13 (-0.009, 0.269)			
Texas	1	Score	No	109	-0.007 (-0.018, 0.004)	0.065 (0.037, 0.093)	0.298 (0.276, 0.319)	0.068 (0.02, 0.116)			
			Lower	12	-0.005 (-0.059, 0.049)	0.113 (0.014, 0.212)	0.327 (0.253, 0.401)	0.14 (0.021, 0.259)			
		Point	Upper	12	-0.035 (-0.091, 0.020)	0.003 (-0.085, 0.091)	0.232 (0.173, 0.292)	0.06 (-0.041, 0.161)			
			Lower	13	-0.015 (-0.061, 0.031)	0.073 (-0.029, 0.174)	0.297 (0.218, 0.376)	0.106 (-0.001, 0.213)			
	2	Score	Upper	12	-0.029 (-0.092, 0.035)	0.016 (-0.065, 0.098)	0.248 (0.191, 0.304)	0.056 (-0.072, 0.184)			
			Lower	15	0.011 (-0.046, 0.067)	0.11 (0.026, 0.195)	0.32 (0.252, 0.387)	0.128 (-0.003, 0.259)			
		Point	Upper	15	-0.039 (-0.064, -0.014)	0.117 (0.047, 0.186)	0.3 (0.251, 0.349)	0.142 (0.022, 0.262)			
			Lower	13	-0.01 (-0.050, 0.029)	0.131 (0.043, 0.218)	0.334 (0.269, 0.399)	0.156 (0.01, 0.302)			
3	Score	Upper	11	-0.061 (-0.095, -0.027)	0.045 (-0.044, 0.134)	0.247 (0.184, 0.309)	0.04 (-0.071, 0.151)				
		Lower	9	-0.027 (-0.123, 0.069)	0.049 (-0.084, 0.183)	0.261 (0.168, 0.354)	0.064 (-0.049, 0.177)				

Table 4.3 Continued.

Study area	Age	Trait	Class	N	Relatedness		Internal relatedness		Homozygosity		F_{is}
					Mean (95% CI)	Mean (95% CI)	Mean (95% CI)	Mean (95% CI)	Mean (95% CI)	Mean (95% CI)	
Texas	3	Score	Upper	9	-0.005 (-0.098, 0.088)	0.06 (-0.093, 0.214)	0.283 (0.179, 0.387)	0.099 (-0.03, 0.228)			
		Point	Lower	4	-0.105 (-0.243, 0.034)	0.083 (-0.045, 0.211)	0.279 (0.141, 0.417)	0.117 (-0.144, 0.378)			
			Upper	10	0.004 (-0.077, 0.085)	0.098 (-0.01, 0.206)	0.3 (0.228, 0.372)	0.099 (-0.034, 0.232)			
	N/A	NT ¹	Absent	134	-0.013 (-0.025, -0.001)	0.077 (0.049, 0.105)	0.287 (0.266, 0.307)	0.093 (0.032, 0.154)			
			Present	22	0.019 (-0.021, 0.059)	0.111 (0.058, 0.164)	0.311 (0.272, 0.351)	0.099 (0.009, 0.189)			
	N/A	Abn ²	Yes	5	-0.063 (-0.138, 0.011)	0.101 (-0.068, 0.279)	0.3 (0.163, 0.437)	0.204 (-0.06, 0.468)			
			No	239	-0.008 (-0.016, 0.000)	0.082 (0.062, 0.102)	0.29 (0.276, 0.305)	0.094 (0.039, 0.149)			

¹ Non-typical points

² Abnormal antlers

Table 4.4. Individual internal relatedness (IR) and homozygosity weighted by locus (HL) scores of white-tailed deer with antler malformations from Oklahoma (1991-2005) and Texas (1999-2005). Sign indicates whether individual deer score was below (<), above (>) or within (=) the 95% CI calculated for deer with normal antlers from its corresponding population (cf. Table 4.3).

Study area	Age	<u>Internal relatedness (IR)</u>		<u>Homozygosity (HL)</u>	
		Score	Sign	Score	Sign
Oklahoma	3	-0.022	<	0.199	<
	2	0.207	>	0.403	>
	2	0.135	>	0.341	>
	1	0.258	>	0.447	>
	1	0.068	=	0.274	<
	1	0.040	=	0.285	=
	3	0.147	>	0.353	>
Texas	4	-0.032	<	0.181	<
	2	0.404	>	0.526	>
	2	0.027	<	0.246	<
	6	0.167	>	0.318	>
	8	0.099	=	0.347	>

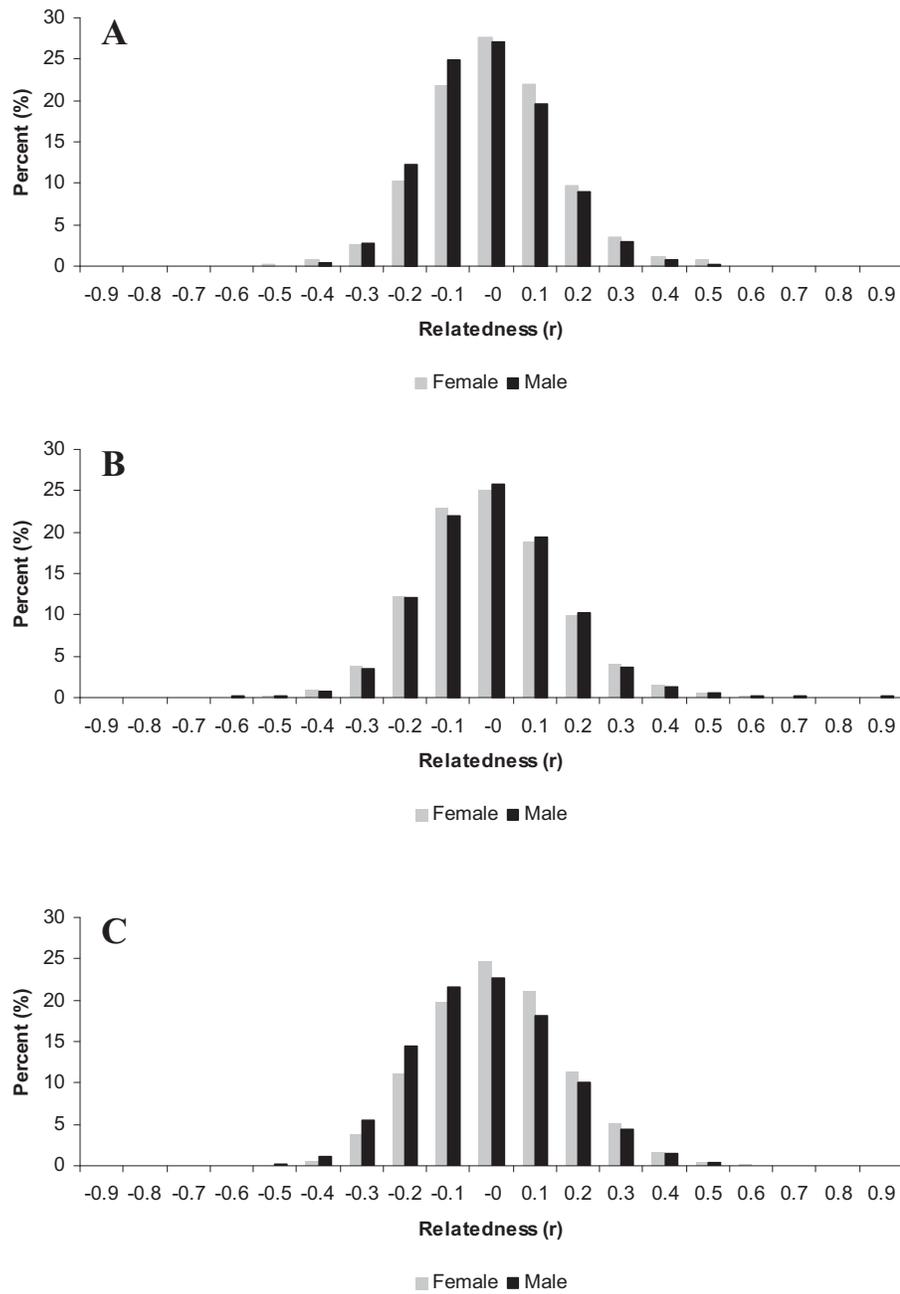


Figure 4.1 Distribution of pairwise relatedness (r) estimates of female and male white-tailed deer from Mississippi (A; 1999-2001), Oklahoma (B; 1991-2005) and Texas (C; 1999-2005).

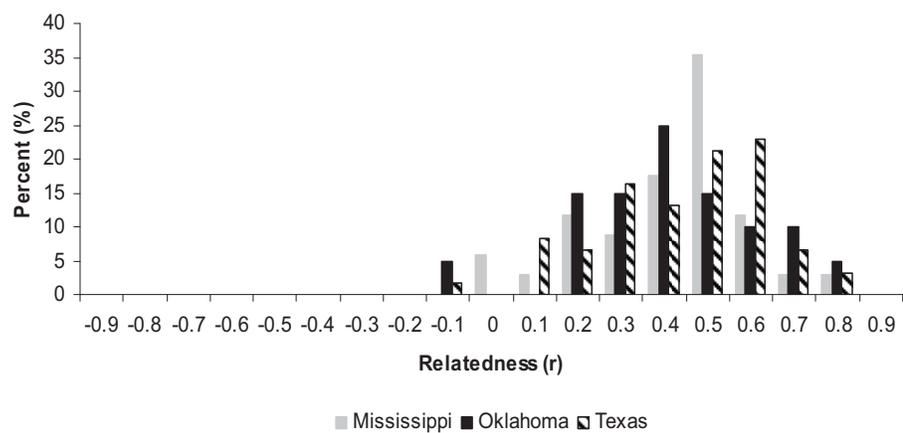


Figure 4.2 Distribution of pairwise relatedness (r) estimates of known sibling pairs from Mississippi (1999-2001), Oklahoma (1991-2005) and Texas (1999-2005).

CHAPTER V
EFFECTS OF SELECTIVE HARVEST ON ANTLER SIZE IN
WHITE-TAILED DEER: A MODELING APPROACH

ABSTRACT

Selective harvesting in wild deer (*Odocoileus* spp.) populations is a common practice that may potentially influence antler size. However, in free-ranging populations, response due to selection is unknown or difficult to quantify because antlers are positively influenced by nutrition and population demographics. I used quantitative genetics models to determine how white-tailed deer (*O. virginianus*) antlers responded to selection and what variables (i.e., population size, age structure, mating ratio and heritability) were most influential in improving antler size. I validated my genetics models by comparing my results with a controlled deer breeding program; modeled antler points (AP) and score increased (2.2-4.3 AP and 48.5-97.7 cm, respectively) after 8 years of selection, similar to observed increases in AP (3.2) and score (92.3 cm) from a captive reference population. In modeled free-ranging populations, mating ratio, age structure and heritability were more important in influencing antler size than size of the population. However, response to selection in free-ranging populations was lower (0.1-0.9 AP) than breeding operations even after 20 years of selection. These data show that selective harvesting of white-tailed deer may be inefficient to modify population-level genetic

characteristics related to antler size. Response in free-ranging deer will be lower because individual reproductive success is lower, breeding is done by a large group of males, and reproductive and survival rates are lower; all of which reduce the amount of improvement that can be made to antlers due to selection. Therefore, selective harvesting should be justified only for controlling population numbers and improving cohort antler size but not for changing the genetic characteristics of free-ranging populations.

INTRODUCTION

The consideration of genetic factors in designing management strategies for white-tailed deer (*Odocoileus virginianus*) populations has increased (Rollins 1998), specifically as it relates to selection and culling (Lockwood et al. 2007). Few studies are available pertaining to selective harvesting in other large ungulates (Kruuk et al. 2002, Coltman et al. 2003, Garel et al. 2007) and there is much to be learned about the genetic consequences of selective harvesting (Harris et al. 2002, Festa-Bianchet 2003, 2008). Long-term studies are needed to detect genetic changes due to selective harvesting (Allendorf et al. 2008), particularly in white-tailed deer.

Selective harvest typically is biased towards males with preferred phenotypes (e.g., antlers or horns) (Festa-Bianchet 2008), but “culling” of animals with small phenotypes also occurs. Selective harvesting of less preferred phenotypes intends to change the underlying gene frequencies of the population (Falconer and Mackay 1996) in favor of large phenotypes by increasing breeding opportunities of these individuals. Changes in gene frequency are typically hidden; thus, response to selection is observed

through changes in the population mean of the phenotypic trait (Falconer and Mackay 1996).

Ungulate populations exposed to selective harvesting of males have changed phenotypic expression, but genetic changes have not been documented. For example, bighorn sheep (*Ovis canadensis*) horn size declined after selective harvest of younger bighorn rams with rapidly growing horns (Coltman et al. 2003). Mouflon sheep (*Ovis gmelini musimon*) horn size and shape were also negatively affected by phenotype-based selective harvest practices (Garel et al. 2007). In white-tailed deer, antler-based selective harvest criteria allowing harvest of young males with larger antlers and protection of smaller-antlered young males reduced mean cohort antler size in subsequent years (Strickland et al. 2001, Demarais et al. 2005).

Selective harvesting white-tailed deer may not elicit phenotypic responses as quickly as bighorn sheep or elk (*Cervus elaphus*). Although white-tailed deer have a polygynous mating system, they do not form harems or display lek mating strategies (DeYoung et al. 2009). Annual and lifetime reproductive success is limited (Sorin 2004, DeYoung et al. 2006, DeYoung et al. 2009) due to searching and tending behavior associated with estrous females (Hirth 1977), short conception period (Marchinton and Hirth 1984) and female promiscuity (DeYoung et al. 2002, Sorin 2004, DeYoung et al. 2006). In addition, antlers are influenced by annual environmental conditions and the individual's nutritional state (Lukefahr and Jacobson 1998, Kruuk et al. 2002). The complexity and interaction of the aforementioned factors makes it difficult to determine the genetic response of antlers to selection in free-ranging deer populations.

Selective breeding and culling have produced substantial improvements in antler size of white-tailed deer confined to captivity. In captive deer breeding facilities in Texas, antler size and points increased after only 8 years of selection (Lockwood et al. 2007). Interest in selective breeding has increased due to the notion that genetically superior deer can be produced (Cooke 1998), but this improvement has not been documented in free-ranging deer populations because it is difficult to separate genetic from environmental responses.

Thus, it is necessary to determine how selective harvest of white-tailed deer might influence antler phenotype. Modeling is one approach to accomplish this task and may be applicable for predicting when and if selective harvest can change population-level phenotypes (Allendorf et al. 2008). However, previous work used unrealistic models (Thelen 1991) or prediction equations (i.e., breeder's equation; Falconer and Mackay 1996) to quantify the effects of selection on antler size. Despite some model limitations, early model simulations elucidated the potential genetic (Thelen 1991) and biological (Strickland et al. 2001) consequences of antler-based selective harvesting practices. In addition, models should be validated (Thelen 1991) using empirical data.

To overcome limitations of previous models, I employed a modeling approach based on quantitative genetics theory for transmission of genetic effects between generations, which is more realistic. Results come from realizations of genetic change due to the propagation process, and are not dependent on simplifying assumptions usually required to make predictions of genetic change. My models are a realization of the selection and propagation processes, which is determined through stochastic simulations

(Kinghorn 1992). I undertook a series of modeling exercises to: 1) validate models prior to their use for free-ranging populations using an 8-year selection experiment from a captive deer population in Texas (Lockwood et al. 2007), 2) determine response of antlers to selection given changes in population size, mating success, age structure and heritability, and 3) determine which parameters were most influential in eliciting a response to selection.

METHODS

Computer program

I used GENUP 5.3 (Kinghorn 1992) and the POPSIM module to simulate the response to selection on white-tailed deer antler size. Modules within GENUP are algorithm-based rather than information-based, which allows the user to adjust parameters to simulate different scenarios (Kinghorn 1992). The POPSIM module draws on parameters entered into the database to generate a population with overlapping generations. A foundation population is generated and then propagated according to a single-trait selection policy chosen by the user. Specifically, the model included the following input parameters: trait mean and standard deviation, heritability, year effect standard deviation, population size, sires/dam (i.e., mating ratio), distribution of number of offspring weaned/female, and annual survival. Model parameter values came from existing datasets or published literature. Additional settings were: selection on individual

phenotype (not using information from relatives to help evaluate each male), mate allocation (i.e., random or assortative), and culling across adult age groups.

Models

I modeled 2 types of management scenarios for white-tailed deer using stochastic model simulations. First, I modeled response of antlers to selection under controlled breeding conditions similar to captive breeding pens in central Texas (Lockwood et al. 2007) as a means of validating modeling approach and parameters. In breeding pens, males can be selected based on phenotype and females based on pedigree data. Therefore, selection in breeding pens can be made on both males and females.

Second, I modeled response to selection under free-ranging conditions where deer population size, age structure, mating success and heritability were varied. Selection in free-ranging populations is only applied to males and reproductive success is limited (Sorin 2004, DeYoung et al. 2006, DeYoung et al. 2009). Therefore, mean response for free-ranging conditions will be less than modeled because selection intensity (i) will be greater on males.

Antler size and heritability

Captive validation

I used antler points (AP) as the dependent variable because heritability values for antler points were available (Williams et al. 1994, Lukefahr and Jacobson 1998). In

addition, selection for antler score in white-tailed deer resulted in a 3.2 mean increase in AP for a captive reference population (Lockwood et al. 2007). Thus, I used average AP in 1.5 year-old males from the captive reference population to validate accuracy of my model. Within the model, antler points were stochastic and normally distributed around the mean based on the standard deviation. Average number of AP for 1.5 year-old males prior to selection was 4.2 ± 1.9 SD (M. Lockwood, Texas Parks and Wildlife Department, personal communication).

I used narrow-sense heritability (h^2) from published data as a deterministic value. Narrow-sense heritability is the ratio of additive genetic variance to phenotypic variance and expresses the extent to which phenotypes are determined by genes transmitted from parents to offspring (Falconer and Mackay 1996). I varied heritability from 0.35, similar to antler points in Lukefahr and Jacobson's (1998) study to 0.7, similar to antler mass and basal circumference in another (Williams et al. 1994).

Free-ranging

I used AP to assess response to selection for free-ranging populations. I used average number of AP from 7 populations with ≥ 6 years ($\bar{x} = 8.4$ years ± 2.3 SD) of data and ≥ 10 samples of 3.5 year-old males/year. All populations were located in the Upper Coastal Plain of Mississippi (Pettry 1977) and deer age was estimated using tooth replacement and wear techniques (Severinghaus 1949). Average number of AP for 3.5 year-old males was 7.3 ± 0.4 SD (B. K. Strickland, Mississippi State University, unpublished data). Heritability was also modeled at 0.35 and 0.7.

Population size and mating rates

Captive validation

Captive breeding pen populations consisted of 5-6 breeding pens with 1 yearling male/pen and 8-16 breeding females/yearling male (Lockwood et al. 2007). For modeling purposes, I allowed each yearling male ($n = 6$) to mate with 12 females ($n = 72$). Yearling males that exhibited the best antler size were used as herd sires for 1 year.

Free-ranging

All free-ranging population characteristics were considered deterministic. Populations had overlapping generations, with individuals of different ages and at different stages in their reproductive cycles. Population sizes of free-ranging deer were modeled at 100, 500, and 1,000 individuals. Population size only reflects the number of breeding individuals (i.e., yearlings and adults) in the population and does not consider young of the year (i.e., fawns). For each population size, I ran models with mating ratios 1:1 (male:female) and 1:3 to mimic targeted pre-harvest sex ratios under conservative deer management programs. In populations with a 1:1 mating ratio each male mated with 1 female/year, whereas in populations with a 1:3 mating ratio, each male mated with 3 females/year.

Age structure

Captive validation

Age structure for captive simulations was similar to the referenced captive facility (Lockwood et al. 2007). Females bred until 7.5 years of age (last fawn born at 8 years of age) or death due to natural mortality or until removed (i.e., culled), whereas males only bred as yearlings (last fawn born at 2 years of age) and were removed prior to breeding the following year.

Free-ranging

Free-ranging populations were modeled using 2 age structures. A young age structure was used to simulate a scenario where harvest is more intense, such as on public landholdings. Older age structures simulated areas with more intensive management to balance age structures by limiting hunter access or harvest rate. Individuals in the young age structure survived to breed through 3.5 years of age with the last offspring born when individuals were 4 years. The old age structure allowed individuals to breed through 7.5 years with their last offspring born when individuals were 8 years. Individuals remained in the population if they met selection criterion. Individuals were removed from the population in 3 ways: natural mortality, culled due to age (i.e., culled after breeding at 7.5 years of age) or culled due to the phenotypic selection criterion at all ages.

Breeding age and recruitment

Captive validation

Age at first breeding was set at 1.5 years for males and females, with their first offspring born at 2 years of age. Average offspring weaned/female varied depending on whether the female was bred as a yearling or adult. The proportion of females bred as yearlings weaning 0, 1 or 2 offspring was modeled at 0.18, 0.37 and 0.45, respectively for penned situations (D. Prochaska, Texas Parks and Wildlife Department, personal communication). For adult females, the proportion weaning 0, 1 or 2 offspring was 0.09, 0.35 and 0.56, respectively (D. Prochaska, Texas Parks and Wildlife Department, personal communication). Based on proportions of 0, 1 or 2 offspring weaned, I found offspring:female ratios were 1.27:1 and 1.47:1 for yearlings and adults, respectively.

Free-ranging

Age at first breeding was also set at 1.5 years of age with offspring weaned/female varying depending on female age. I derived estimates of proportion weaned in free-ranging populations from the proportion of fetuses/yearling and adult females collected during annual spring health checks in Mississippi (B. K. Strickland, Mississippi State University, unpublished data) and fawn mortality rates to 180 days. Percentage of females bred as yearlings (n = 554) having 0, 1 or 2 offspring was 2, 64 and 34%, respectively whereas the percentage of adult females (n = 3,550) with 0, 1 or 2 fetuses was 1, 22, and 77%, respectively (B. K. Strickland, Mississippi State University,

unpublished data). I selected a 43% survival rate to 180 days, similar to Kunkel and Mech (1994), Long et al. (1998), and Ballard et al. (1999). To simulate pre-weaning fawn mortality, I assumed 50% of females with 2 offspring lost 1 offspring, whereas the remaining 7% (cumulative loss = 57%) lost both offspring. Thus, in free-ranging populations, 0.41, 0.44 and 0.15 of yearlings and 0.19, 0.48 and 0.33 of adults weaned 0, 1 and 2 offspring, respectively. Based on proportions of 0, 1 or 2 offspring weaned, I found offspring:female ratios were 0.74:1 and 1.14:1 for yearlings and adults, respectively.

Survival

Captive validation

Survival of captive deer from birth to 1.5 years of age was 55% for females and 61% for males and survival from birth to weaning was 74% (both sexes combined; Lockwood et al. 2007). I derived survival from weaning to 1.5 years of age because an estimate of post-weaning survival was needed for model simulations. The following formula was used to derive survival from weaning to 1.5 years:

$$S_{\text{total}} = S_1 * S_2 \tag{5.1}$$

Where:

S_{total} = survival from birth to 1.5 years

S_1 = survival from birth to weaning

S_2 = survival from weaning to 1.5 years

For instance, male survival was estimated by the formula: $0.61 = 0.74 * S_2$. Rearranging the formula to solve for S_2 gives $S_2 = 0.61/0.74$ and a survival estimate of 0.82. Thus, survival rates were modeled at 74% and 82% for females and males, respectively.

Free-ranging

Annual survival for free-ranging males and females came from recently published literature. Webb et al. (2007a) followed a known-aged cohort of males from 1.5 through 6.5 years of age and found average annual survival was 82%; harvest of radio-collared deer was restricted so all mortalities were considered natural. Average annual survival of yearling and adult female white-tailed deer was 87% (Campbell et al. 2005), which is similar to average annual survival of female cervids (89%) reviewed in Gaillard et al. (2000). Therefore, male survival was set at 82% and female survival at 89%. In model simulations, survival is random with respect to phenotype, so some of the most superior individuals, in terms of phenotype, were lost to mortality.

Year effect

Environmental effects for year of birth on expression of phenotype can be fitted in Popsim with subsequent selection on “corrected phenotype” or “best linear unbiased prediction” (both selection criterion options). However, these effects were not included in the calculation of phenotypes in Popsim because year of birth could not be estimated for free-ranging samples used to calculate mean number of AP. The inaccuracy of

estimating age of deer past 1.5 years using tooth replacement and wear (Gee et al. 2002) precludes assignment of deer to specific year of birth. Additionally, h^2 estimates typically account for year of birth effects on the phenotypic variance (Lukefahr and Jacobson 1998). Therefore, I did not incorporate environmental effects for year of birth into captive or free-ranging model simulations.

Selection criterion

The selection criterion for both captive and free-ranging simulations was set to phenotypic selection, which removed individuals with the fewest AP. This selection acted across age classes due to choice of the parent selection option. The number of males and females removed was dependent on the number of males and females recruited into the population, which is similar to typical management goals of free-ranging populations. In white-tailed deer, only males possess antlers, the phenotypic trait of interest; therefore, I made selections only on the male phenotype in free-ranging population models. To correct for phenotypic selection on males only in free-ranging populations, I calculated sex-specific selection intensities (i) based on the proportion (p) of each sex selected for breeding from the set of candidates (Appendix A of Falconer and Mackay 1996) as follows:

$$p_m = M_{\text{select}}/M_{\text{cand}} \quad (5.2)$$

$$p_f = F_{\text{select}}/F_{\text{cand}} \quad (5.3)$$

Where:

$$p_m = \text{proportion of males selected}$$

M_{select} = number of males selected for breeding

M_{cand} = number of male candidates available for breeding

M_{cand} was calculated as the number of male fawns weaned multiplied by male survival rate, p_f = proportion of females selected, F_{select} = number of females selected for breeding, and F_{cand} = number of female candidates available for breeding, which was calculated as the number of male fawns weaned (which assumed a 50:50 sex ratio at birth and equal pre-weaning mortality) multiplied by female survival rate. The number of candidates available for each sex is equal to the number of breeders already present plus the new set of candidates. Overall i (i_o) was calculated as:

$$i_o = (i_m + i_f) / 2 \quad (5.4)$$

Where:

i_m = selection intensity of males

i_f = selection intensity of females

Male only selection intensity (M_i) was calculated as:

$$M_i = (i_m + 0) / 2 \quad (5.5)$$

Selection intensity ratio (i_r) was calculated as:

$$i_r = M_i / i_o \quad (5.6)$$

Selection intensity ratio (i_r) was used to correct response to selection by multiplying i_r by observed response. For captive simulations, I used the mean response/year calculated because females could be selected based on pedigree data and males based on phenotype. However, mean response/year in captive simulations is an approximation because accuracy (i.e., correlation between phenotype and true breeding value) would be reduced for females because females do not possess antlers and are selected based on pedigree data.

Mating system

Captive validation

I used assortative mating, which is an artificial mating strategy where individuals with similar phenotypes are mated together to simulate captive deer facilities. Selection criterion was set to phenotype to take into account males are selected based on antler size and mating system was set to assortative to take into account that females were selected based on pedigree data. Therefore, the best males and females should be mating together in the penned simulations.

Free-ranging

Random mating was used for all free-ranging simulations. With random mating all individuals in a population have an equal probability of mating with any other individual.

Selection type

Selection type was set to “parent selection” for both captive and free-ranging populations. Under this option, adult animals have to compete with each other and with the yearling cohort to remain in the breeding population. Under the alternative “progeny selection” option, adults are never culled on merit once they have been selected as yearlings.

Model assumptions

Response to selection depends on h^2 in the generation from which the parents were selected, so response to selection is dependent on h^2 , which for prediction purposes should be recalculated each generation (Falconer and Mackay 1996). However, my simulations are not calculated predictions, but observed realizations. The estimates of heritability supplied were used to sample genetic effects of the foundation parents and segregation genetic effects in each full sib family generated thereafter. This scheme accommodates loss of genetic variance due to selection (whereby selected parents are more similar to each other genetically than if they were chosen at random). Loss of variation due to inbreeding and the associated approach to fixation of alleles is also accommodated, even though individual genes are not simulated. This is because genetic effects are generated contingent on the inbreeding coefficients of contributing parents, with zero segregation variance for fully inbred parents.

Selective harvest programs for male white-tailed deer typically take both inferior (i.e., cull) and trophy deer. Popsim only removes inferior deer leaving all trophy deer to

breed. Because this is unrealistic in most managed free-ranging populations of white-tailed deer, my models provide a “best case” scenario for improving antler size.

Selective harvest programs also vary based on which ages are culled from the population. In Popsim, phenotype (i.e., AP) potential was generated at random but was contingent on the parents’ true breeding values (B. Kinghorn, University of New England, personal communication). Phenotype potential assigned number of AP at the maximum age of males in model simulations (i.e., 3.5 and 7.5 years) to males at birth. Thus, phenotype potential was available for yearling males when they first reached reproductive maturity. Therefore, I assumed that yearling antler size and adult antler size were highly correlated (Demarais 1998; Ott et al. 1998) allowing yearling antler size to be a selection criterion for removal. Therefore, males with inferior phenotypes (i.e., AP) from each age group were culled from the population with adult males competing against yearling males with assigned phenotype potential. This assignment of AP potential would result in increased response because males could be identified at an early age as to their true phenotypic quality.

I also assumed that reproductive rate, age structure, and annual survival probability were constant, which in free-ranging populations likely fluctuates from year-to-year. Higher reproductive rates (i.e., offspring weaned/female) of the population result in greater selection intensity. Because reproductive rate partially dictates selection intensity, the proportion selected for breeding can never be less than the proportion needed for replacement (Falconer and Mackay 1996), if breeding population size is to be maintained. The longer parents are kept, the longer the generation interval, contributing

to decreased selection response per year. However, longer lived individuals will have a greater probability of contributing offspring to the next generation (Falconer and Mackay 1996), which results in stronger selection intensity, and a positive contribution to selection response. These opposing effects mean that there is an intermediate age structure that is optimal for speed of response per year.

Mating success varies with population demographics, but was not skewed toward a few individuals or related to phenotypic characteristics (Sorin 2004, DeYoung et al. 2006, DeYoung et al. 2009). For instance, males obtaining successful copulations had antler sizes similar to their age-specific cohort averages (Sumners et al. 2007, J. A. Sumners, Texas A&M University-Kingsville, unpublished data). Additionally, when adult sex ratios were skewed in favor of females, males of all ages had more uniform reproductive success (Pemberton et al. 1999; DeYoung et al. 2009). Therefore, I assumed that males, regardless of age and antler size, had the same mating success within each population of a given mating ratio. For example, in a population with a 1:3 mating ratio, each male would mate with 3 females. Because females may have 0-2 offspring and offspring may be lost to natural mortality, actual reproductive success (i.e., offspring recruited) did vary, but not in relation to antler size.

As population size increases, the absolute number of deer to be removed will also increase. In free-ranging populations it may be near impossible, due to logistics, to harvest enough individuals to maintain the target population size. My models removed all individuals exceeding the number required for replacement, even though this may not be feasible when managing large free-ranging populations (Stedman 1998).

I assumed no migration (i.e., immigration or emigration). In populations subject to immigration, the rate of gene frequency change depends on the immigration rate and the difference between gene frequencies of the immigrants and the original population (Falconer and Mackay 1996).

Analysis

Proportion removed

Total animals (i.e., males and females) weaned each year before death or culling was reported in the output window of POPSIM (years available equals age when last offspring was born). I recorded 4 or 8 year means of number of males weaned for each run ($n = 20$) within a model ($n = 28$). To take into account mortality from weaning to 1.5 years, I multiplied each value by S_m (S_m = annual male survival). The mean percentage of males removed (i.e., culled) was based on the following formula for captive simulations where only males were selected each year from the newly recruited yearlings:

$$PR_{\text{mean1}} = |(B_m / YP_{\text{mean}}) - 1| * 100 \quad (5.7)$$

Where:

B_m = number of breeding males needed

YP_{mean} = mean number of yearling males produced

PR_{mean1} = mean percentage of males removed

I used the following formula to calculate the mean percentage of males removed from free-ranging simulations where breeding males were selected from the current population of males and from the newly recruited males:

$$PR_{\text{mean2}} = |((B_m / (YP_{\text{mean}} + B_{\text{mp}})) - 1) * 100 \quad (5.8)$$

Where:

- B_m = number of breeding males needed
- YP_{mean} = mean number of yearling males produced
- B_{mp} = number of breeding males already present
- PR_{mean2} = mean percentage of males removed

Means and SD of $PR_{\text{mean1,2}}$ were calculated over each set of 20 runs within model for reporting purposes.

Statistical analysis

I used stepwise multiple regressions to determine which explanatory variables were most influential in changing antler size (PROC REG; SAS Institute 2003).

Explanatory variables in free-ranging model simulations included population size, age structure, mating ratio (i.e., dams/sire), and heritability. For each free-ranging model ($n = 24$), only 1 explanatory variable was changed. However, I used each run ($n = 20$) to incorporate stochastic variation among runs within a particular model. I used $\alpha = 0.05$ for addition of variables into the model and also for retaining variables in the model. I used partial coefficients of determination (R^2) to determine which variable(s) had the largest

influence on response to selection. Regression analyses were conducted using SAS 9.2 (SAS Institute 2003). Residual and normal probability plots were used to ascertain whether assumptions were met.

Composite measure of antler size

A composite measure of antler size is commonly used for determining total antler size in deer. In most cases, gross Boone and Crockett antler score (hereafter antler score) is used, which is a measure of inside spread between main beams, main beam length of right and left antlers, circumference of main beams at 4 locations on each antler, and total length of all points ≥ 2.54 cm (Boone and Crockett Club 1997). Heritability estimates are only available for the individual components of antler score (Williams et al. 1994, Lukefahr and Jacobson 1998). Because antler score increased due to selection for this antler trait in Texas (Lockwood et al. 2007), I wanted to test my model to determine how well model results fit to observed increases in antler score. If model results are similar, a composite measure of antler size (i.e., antler score) may be more useful for future modeling efforts because antler score is a more accurate reflection of the total antler size of deer compared to AP because it is a composite of multiple measurements and is a continuous trait. Yearling antler score of the reference captive deer population during the first year of the study (i.e., prior to selection) was 100.3 ± 44.7 cm (39.5 ± 17.6 inches; M. Lockwood, Texas Parks and Wildlife Department, personal communication), which was used for model simulations.

RESULTS

Captive validation

Selection for increased AP resulted in greater number of AP on 1.5 year old males after 8 years, or 2.7 generations, of selection. Antler points improved by 4.3, increasing from 4.2 to 8.5 (± 0.4 SD) when h^2 was modeled at 0.7 (Table 5.1). When h^2 was modeled at 0.35, AP increased by 2.2, from 4.2 to 6.4 (± 0.4 SD; Table 5.1). Mean percentage of males removed averaged 85.4 (± 0.6) and 85.2 (± 0.9) for models using $h^2 = 0.35$ and 0.7, respectively (Table 5.1).

Free-ranging simulations

Selection on AP resulted in positive increases in number of AP across all models ($n = 24$; Table 5.1). Antler points ranged from 7.4-8.2 after 20 years of selection (5.5-7.2 generations), which was an increase of 0.1-0.9 AP from the starting population mean ($\bar{x} = 7.3$; Table 5.1). Mean percent of deer removed (i.e., culled) each year ranged from 28.2-56.0% across simulations (Table 5.1). Mean percent of males removed was 89% greater when the mating ratio was 3 dams/sire ($55.4\% \pm 1.2$ SD) compared to 1 dam/sire ($29.3\% \pm 1.2$ SD).

Stepwise regression models selected 3 of 4 explanatory variables; mating ratio (dams/sire), male age structure, and heritability were included whereas population size was not. There was a positive relationship between antler points and all 3 model variables. Mating ratio accounted for the most variation (0.54), followed by heritability

(0.25) and male age structure (0.12). The final regression model, with the 3 explanatory variables, accounted for 91% of the variation in final number of AP after 20 years of selection.

The regression equation, $AP = 6.64 + 0.046(\text{age}) + 0.2(\text{dams/sire}) + 0.785(h^2)$, can be used to predict the number of AP after 20 years of selection. However, I was also interested in predicting response to selection by year. Thus, I incorporated the number of AP after 5, 10, 15 and 20 years of selection into my model with male age structure, mating ratio, and heritability. The final regression model, $AP = 6.62 + 0.03(\text{age}) + 0.131(\text{dams/sire}) + 0.512(h^2) + 0.02(\text{year})$, then could be used to predict response to selection at any given year.

Selection on antler score

Modeled selection for increased yearling antler score also resulted in positive gains after 8 years of selection in captive breeding facilities. Antler score increased by 97.7 cm from 100.3 cm (± 44.7 SD) to 198.0 cm ± 14.8 SD when h^2 was modeled at 0.7. When h^2 was modeled at 0.35, antler score increased by 48.4 cm to 148.7 cm ± 12.9 SD. Mean percentage of males removed averaged 85.5 (± 0.6) when $h^2 = 0.7$ and 85.4 (± 0.7) when $h^2 = 0.35$.

DISCUSSION

Models developed in Program GENUP provided flexibility in simulating a wide range of scenarios from captive breeding operations to large free-ranging populations.

Both empirical and model results revealed similar findings; response to selection was faster and greater in controlled situations. For example, captive breeding facilities increased mean number of AP by 3.2 and antler score by 92.3 cm after only 8 years (2.7 generations) of selection (Lockwood et al. 2007). Model simulations also resulted in improvements in AP and score and were similar to observed values of the reference population, which offers support that model results would be an accurate reflection of the process of selection in free-ranging populations.

Antler score is a composite measure of total antler size comprised of several independent components (i.e., inside spread, main beam length, circumferences, and antler point length) but has no measure of heritability associated with it. Because most individual components of antler score are heritable (Williams et al. 1994, Lukefahr and Jacobson 1998), antler score may be improved through selection as well. By selecting for increased antler score in captive facilities, researchers were able to increase antler score and all individual components of antler score (Lockwood et al. 2007). Model simulations also resulted in increased antler scores after selection for larger antlers (i.e., score). Antler score may be a more useful measure of total antler size than AP in white-tailed deer because antler score is a composite measure of several antler traits and has a continuous range of values.

Contrary to findings from captive simulations, selection for increased AP in free-ranging populations did not result in significant improvements, even after 20 years (5.5-7.2 generations) of selection. Modeled free-ranging populations differed markedly from captive populations. In general, the amount of control over the breeding population is

greater in captive facilities where information (i.e., phenotypes and pedigrees) is available on males and females and mating can be tightly controlled (i.e., dams/sire) leading to better mating strategies (e.g., assortative mating). In free-ranging populations, information is only available for males (i.e., phenotype), mating is random, and mating success cannot be controlled, only targeted (i.e., sex ratio).

Contrary to captive populations, the basic selection pressures responsible for phenotypic change in free-ranging populations are only approximations of a specific targeted value for mating success, age structure, and population size. Mating success was found to contribute to response of antler size to selection in free-ranging model simulations. However, mating success cannot be controlled, only targeted through variations in sex ratios. Mating success was found to vary with demographics of the population (Sorin 2004, DeYoung et al. 2006, DeYoung et al. 2009). However, reproductive success was not related to phenotypic characteristics; successfully mating males had antler sizes similar to their age-specific cohort averages (Sumners et al. 2007). Most importantly, when adult sex ratios were skewed in favor of females, males of all ages had more uniform reproductive success (DeYoung et al. 2009), which is similar to other polygynous ungulates (Pemberton et al. 1999). Soay sheep (*Ovis aries*) males of all ages had increased mating success at low population sizes and sex ratios, which resulted from male-biased populations crashes (Pemberton et al. 1999). Thus, if males with inferior antlers can be selectively removed prior to breeding, leaving only males with above average antlers to breed, then the remaining breeding males may have more uniform mating success. However, in most free-ranging populations it would be

impossible to remove all inferior males prior to the breeding season. In addition, some trophy males are harvested prior to mating, which does not allow these trophy males to contribute offspring to future generations. These opposing forces (i.e., harvest of both inferior and trophy males) reduce response to selection because individuals more similar to the mean antler size are having greater mating success (e.g., stabilizing selection).

Male age structure varies in accordance with management objectives or is a direct result of the amount of harvest applied to the male segment of the herd. Younger male age structures often result from intense harvest pressure whereas older male age structures result from limited harvest or hunter access. Similar to mating success, male age structure influenced response of antlers to selection. Selection can be optimized by choosing either young or old individuals for breeding (van der Werf 2000a). Older individuals will have a greater chance of contributing offspring to the next generation compared to younger individuals (Falconer and Mackay 1996). This corroborates my findings, as age structure increased so did response of antlers to selection. This was likely the direct result of longer-lived individuals having greater lifetime reproductive success by contributing more offspring to future generations. It may be more difficult for younger males to contribute offspring to future generations because mean individual reproductive success is limited because only 30-33% of 1.5 and 2.5 year-old males collectively sired offspring compared to ≥ 3.5 year-old males (DeYoung et al. 2009). Thus, allowing males with above average antlers to reach older age classes may result in greater reproductive success and recruitment of offspring into the population along with the genes carried by males for antler size.

Population size did not influence response of antlers to selection in model simulations. However, population size may have consequences on the level of inbreeding that occurs within the population. Inbreeding will be more prevalent in small populations because there will be increased opportunities for mating with related individuals, even under random mating (van der Werf 2000b). My models effectively acted as a closed population where no new individuals immigrated into the population; only individuals born into the population were used for mating. This scenario is similar to deer confined within fenced enclosures. The probability of inbreeding within closed populations increases because males do not disperse as far (Honeycutt 1998) and maintain similar home range areas (Webb et al. 2007b, Hellickson et al. 2008), as do females (Tierson et al. 1985, Grund et al. 2002). To reduce the rate of inbreeding some level of gene flow among populations should be maintained (Ryman et al. 1981); however, gene flow from populations with opposing selection pressures may reduce response to selection (Kruuk et al. 2002).

Selective removal of individuals involves 2 additional aspects of selective harvesting: age versus antler size and harvestable surplus. Model simulations assumed yearling and adult antler size were highly correlated (Demarais 1998, Ott et al. 1997, Ott et al. 1998) because my model assigned antler point potential to yearlings. Ott et al. (1997) also noted that yearling antler size must predict adult antler size if selective harvesting was to elicit a response. The assignment of antler point potential allowed inferior phenotypes to be identified at an early age and removed from the population. However, other results from research on white-tailed deer confined to breeding pens did

not recommend using yearling antler size as criteria for selective harvesting (Lukefahr and Jacobson 1998). To obtain response of antlers to selection similar to model simulations, yearling antler size must be highly correlated with adult antler size and males with inferior antlers must be removed at all ages, including yearlings.

In free-ranging populations, it may be difficult to remove the harvestable surplus each year as population size increases due to logistical constraints (Stedman 1998). As population size increases, the absolute number of deer to be removed also increases. Model simulations removed all individuals above replacement, a task difficult to undertake in large, free-ranging populations where recruitment and population size are difficult to estimate. For response to occur, the harvestable surplus of both males and females needs to be removed each year; dependent on each year's target population size and sex ratio, current population size, and recruitment rate. In addition, proportion removed should be similar to, or greater than, the proportion removed in model simulations for an observed response to be detectable.

The lack of observed response in free-ranging populations is complicated by a number of factors. First, heritability in free-ranging populations may differ from captive populations because heritability is affected by environmental variance (Falconer and Mackay 1989), which is likely greater in free-ranging populations (Kruuk et al. 2002). Only one study has revealed heritability of a free-ranging cervid population; heritability of antler mass in red deer (*Cervus elaphus*) was 0.33 (Kruuk et al. 2002), similar to my modeled value (0.35). Captive populations have considerable control over environmental components, allowing environmental effects to be standardized (Walsh 2009) and the true

phenotypic trait to be targeted for selection (e.g., antler size) resulting in rapid response to selection (Lockwood et al. 2007). Modeling a range of heritability values elucidated the influence of additive genetic variance on the response of antlers to selection. Selectively harvesting free-ranging deer to increase antler size will meet resistance due to lack of control of environmental effects, and its influence on heritability.

Second, environmental conditions may mask response to selection if environmental conditions exert an opposing force on the phenotype (Kruuk et al. 2002). For example, selection should have increased response in red deer antler mass, but antler mass decreased due to increased population density (Kruuk et al. 2002), which typically diminishes environmental conditions. Additionally, an environmental correlation may arise due to the effects of date of parturition on antler size. Deer born early typically have greater antler growth (Knox et al. 1991, Shea et al. 1992, Gray et al. 2002) due to increased nutrition and additional time for body development (Gray et al. 2002), so there may not be a heritable aspect to antler size due to the environmental correlations with date of parturition affecting body development. Causey (1990) documented that deer born late had antlers similar in size to early born deer in a captive population due to high quality and quantity feedstuffs. This illustrates the potential for captive breeding facilities to control a portion of the environmental variance related to antler size.

Third, genetic correlations may occur between an unmeasured phenotypic trait (e.g., leg length or body mass) and the trait of interest (i.e., antler size) through pleiotropy (i.e., genes influence multiple traits) or linkage disequilibrium (i.e., non-random association of genes; Lynch and Walsh 1998). Genetic correlations between two traits

may facilitate or impede response to selection depending on how the traits are correlated (Lynch and Walsh 1998). For example, if two genetically correlated traits are selected for (e.g., increased antler and body size), but negatively correlated, then selection for an increase in one trait may drive the second trait in the opposite direction. A negative genetic correlation existed between leg length and antler size in red deer (Kruuk et al. 2002). The lack of response of antler size may have been attributed to the negative genetic correlation with leg length because increased leg length led to higher lifetime reproductive success of stags. However, there was not strong evidence of a negative genetic correlation acting upon selection for increased antler size because SE of the correlation was large, leg length was positively correlated with other antler measures, and predicted response of antlers to selection was still positive after accounting for leg length. This goes to show that detection of genetic correlations may not be sufficient alone to explain a lack of response to selection.

Last, opposing selection pressures on females or animals from surrounding populations may affect response to selection (Kruuk et al. 2002). Female white-tailed deer cannot be harvested based on antler size because only males develop antlers, so females are often targeted for harvest based on body size; larger females are preferentially harvested to smaller females. If females with large bodies unknowingly carry genes for large antler size, then harvest of large-bodied females will act against the positive forces of selection for increased antler size in males. Opposing selection pressures on the two sexes would reduce response of antlers to selection.

Opposing selection may also occur due to gene flow among populations with disparate management goals. Unless a population is confined to impermeable fences or isolated from other populations (e.g., island populations), male deer dispersal (McCoy et al. 2005) and movements (Webb et al. 2007b) will result in deer using large spatial extents, which can allow gene flow to occur among populations. If breeding individuals emigrate into the population from an area with opposing selective pressures, then response will be reduced, but if individuals emigrate from populations with similar selection pressures then response may be improved. For managers of deer populations, creating wildlife cooperatives with nearby properties (Hamilton et al. 1995) may reduce opposing forces of disparate management practices.

MANAGEMENT IMPLICATIONS

It is clear from these data that selective harvesting in free-ranging populations to increase antler size is inefficient and only minimal results should be expected over a 20-year effort. However, managers wishing to attempt selective harvest programs to improve antler size in free-ranging populations should focus on population demographics, such as sex ratios and age structures, and selective harvesting at appropriate times relative to breeding seasons. Only inferior males should be harvested prior to breeding, whereas males with larger antlers should only be harvested at maturity (i.e., ≥ 6.5 years) and after the breeding season. In addition, sex ratios skewed towards females (e.g., 1 M:3 F) may allow trophy males to have more uniform reproductive

success each year allowing trophy males to pass genes for large antler size onto their offspring.

Careful attention should be paid to harvest strategies, particularly when intense selective harvest causes genetic or evolutionary changes (Coltman et al. 2003, Allendorf et al. 2008). Although, phenotypic changes may not be visible, more cryptic genetic changes may be occurring, which warrants observation of genetic variation over time as the population is exposed to selective harvesting. Closed populations require more intense monitoring as gene flow may be limited from surrounding populations; a problem not as evident in large, free-ranging populations where immigration and emigration frequently occur.

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Table 5.1 Response (R) of number of antler points in white-tailed deer (*Odocoileus virginianus*) to simulated selection in captive (8-year selection) and free-ranging populations (20-year selection). Response was a function of mating success (dams/sire), population size, male age structure, and heritability (h^2). Male selection intensity (i) and percentage removed was dependent on the number of males selected for mating and number of candidate males available for mating. Male generation intervals were 2.0, 2.7 and 3.4 for 2, 4 and 8 years, respectively. Female generation intervals were 2.9 and 3.9 for 4 and 8 years, respectively. Population generation intervals were 2.7, 7.2, and 5.5 for the captive population and free-ranging populations with a 4 and 8 year age structure, respectively.

Scenario	Sires	Dams/sire	Population size	Last offspring (m, f)	h^2	Points (\pm SD)	Change	\bar{x} R/yr	i	Percentage removed	
										Mean (\pm SD)	
Captive	6	12	78	2, 8 ¹	0.35	6.4 (0.4)	2.2	0.3	---	85.4	(0.6)
					0.7	8.5 (0.4)	4.3	0.5	---	85.2	(0.9)
					0.35	7.4 (0.1)	0.1	<0.1	0.5	28.2	(1.8)
Free-ranging	50	1	100	4, 4 ²	0.7	7.5 (0.1)	0.2	<0.1	0.5	28.5	(1.6)
	25	3	100	4, 4	0.35	7.7 (0.1)	0.4	<0.1	0.6	55.0	(1.7)
	50	1	100	8, 8 ³	0.7	8.0 (0.1)	0.7	<0.1	0.6	54.4	(2.2)
					0.35	7.5 (0.1)	0.2	<0.1	0.5	30.0	(1.1)
					0.7	7.8 (<0.1)	0.5	<0.1	0.5	30.2	(1.1)
	25	3	100	8, 8	0.35	7.8 (0.1)	0.5	<0.1	0.6	55.8	(1.6)
					0.7	8.2 (0.1)	0.9	<0.1	0.6	55.9	(1.1)

Table 5.1 Continued.

Scenario	Sites	Dams/sire	Population		Last offspring (m, f)	h^2	Points		Change	\bar{x} R/yr	i	Percentage removed	
			size				(\pm SD)					Mean (\pm SD)	
Free-ranging	250	1	500		4, 4	0.35	7.4 (<0.1)	0.1	<0.1	0.5		28.4 (0.7)	
	125	3	500		4, 4	0.7	7.5 (<0.1)	0.2	<0.1	0.5		28.8 (1.0)	
	250	1	500		8, 8	0.35	7.5 (<0.1)	0.2	<0.1	0.5		30.1 (0.6)	
	125	3	500		8, 8	0.7	7.8 (<0.1)	0.5	<0.1	0.5		29.8 (0.4)	
	500	1	1,000		4, 4	0.35	7.4 (<0.1)	0.1	<0.1	0.5		28.7 (0.5)	
	250	3	1,000		4, 4	0.35	7.7 (<0.1)	0.4	<0.1	0.6		54.8 (0.6)	
						0.7	8.1 (<0.1)	0.8	<0.1	0.6		54.8 (0.5)	

Table 5.1 Continued.

Scenario	Sites	Dams/sire	Population size	Last offspring (m, f)	h^2	Points (\pm SD)	Change	\bar{x} R/yr	i	Percentage removed Mean (\pm SD)
Free-ranging	500	1	1,000	8, 8	0.35	7.5 (<0.1)	0.2	<0.1	0.5	30.1 (0.4)
	250	1	1,000	8, 8	0.7	7.8 (<0.1)	0.5	<0.1	0.5	29.8 (0.4)
					0.35	7.8 (<0.1)	0.5	<0.1	0.6	56.0 (0.4)
					0.7	8.2 (<0.1)	0.9	<0.1	0.6	55.8 (0.3)

¹Selection was applied for 2.7 generations

²Selection was applied for 7.2 generations

³Selection was applied for 5.5 generations

CHAPTER VI

SYNTHESIS AND IMPLICATIONS

Management practices for white-tailed deer (*Odocoileus virginianus*) encompass a wide range of techniques. Each management practice must consider behavior of the target species and any potential impacts these practices may have on the species. Management without a priori information on the species' ecology may result in failure. Management may not succeed if there is not a way to assess response of the population to management. Therefore, quantifying the relative effects of each management practice on population responses, whether to reduce movements, increase antler size, or change population demographics, will be crucial to meeting management goals.

Management for white-tailed deer seeks to control their movements such as immigration and emigration rates. Modeling exercises have elucidated the importance of various types of movements (e.g., dispersal, migration, and annual shifts in home range centers) on ability to manage populations at varying property sizes (McCoy et al. 2005, Webb et al. 2007). Findings reveal that relatively large, continuous properties, or management units, are necessary to help control deer movements, which in turn affects interpretation and success of management programs. "Deer-proof" fences often are erected around smaller properties to minimize loss of deer to surrounding properties with differing management programs.

Despite the increasing number of fenced enclosures (Demarais et al. 2002), few studies exist on how high fences affect movement patterns of ungulates. There is concern of the impacts confinement may have on deer behavior (Demarais et al. 2002). Therefore, the first step is identifying basic measures of space use, such as movement distance or rate and home range size, of deer confined to fenced enclosures. I evaluated the effectiveness of a 15-strand high-tensile electric fence (HTEF) to control deer movements. In addition to controlling deer movements, the fence design also needed to have as little influence on deer behavior as possible, as examined by changes in movement patterns.

The HTEF was an effective barrier to deer movements when properly maintained. Deer moved across the fence at weaknesses such as holes or water gaps but when properly maintained, the HTEF controlled the majority of deer movements. Although the fence design was not completely effective at controlling deer movements, it did control a large percentage of the population. Reduced movements across the fence facilitated management without compromising the long-term health of deer. If the goal of the fence is to completely enclose or exclude white-tailed deer, then alternative fence designs or modification of the 15-strand HTEF may be needed. The HTEF also appeared to have little influence on deer spatial dynamics. Deer did not appear to be affected by the HTEF because movements and home ranges were within the range previously reported, had home ranges bordering the fence, and had the ability to expand movements or home ranges within the enclosure if needed.

Movement patterns also did not appear to be affected by enclosure. Similar to previous research, I found white-tailed deer were primarily crepuscular (Michael 1970, Kammermeyer and Marchinton 1977, Beier and McCullough 1990) with greatest movements occurring near sunrise and sunset. Analyzing data on a finer scale than season revealed changes in deer movement patterns relative to parturition and rut for females and males, respectively. Just as deer movement response is related spatial scale of habitat structure (Webb et al. 2009), deer also respond temporally to physiological and environmental changes. Movements and home ranges could be expanded; thus, the size of the study area enclosed by the HTEF was large enough to allow deer movement patterns to be maintained within the range of those previously reported. Thus, enclosure did not dramatically influence space use patterns of deer in this population. However, other factors such as habitat quality may alter how an enclosure impacts deer movement patterns.

Environmental factors, such as weather, may have a stronger influence on deer movements in northern latitudes compared to southern latitudes. Snow depth and temperature consistently affect deer activity and movements in northern latitudes (Loveless 1964, Progulske and Duerre 1964, Rongstad and Tester 1969, Moen 1976, Beier and McCullough 1990), but these factors are not as extreme in southern latitudes. Severe weather coupled with confinement to high fences may be detrimental to deer in northern latitudes, particularly migratory populations. Studies should determine if deer confined to fenced enclosures are more or less affected by environmental factors, even for southern populations that only experience severe weather for short periods.

Seasonal environmental changes appeared to influence movement patterns of deer, whereas fine-scale temporal weather patterns had minimal influence.

Environmental variation may influence activity rhythms in animals (Randall et al. 2002), which was similar to my findings that females adjusted time budgets during the summer to move less over diel cycles, but more during nocturnal hours. This seasonal acclimatization appears to be a behavioral response to reduce heat stress.

Cold temperatures may increase metabolic rate due to thermoregulation and activity (Gates and Hudson 1979). If movements are a thermoregulatory penalty (Gates and Hudson 1979), then deer should avoid moving at night during cold temperatures. Because I did not find this to be true, male deer may move more at night during winter to avoid contact with hunters or mirror movements of receptive females (Kilgo et al. 1998). Therefore, the potential negative effects of increased metabolic rate may be countered by an increase in fitness due to reproductive success.

Although there is much conflicting evidence on the affects of weather on deer movements, most studies have found minimal influence. Many times it is difficult to detect an association between deer movements and weather because deer movements and weather follow seasonal cycles (White and Garrott 1990). However, my analysis approach removed much of the seasonal and daily variation in weather patterns allowing more accurate conclusions to the influence of short-term weather patterns on fine-scale temporal deer movements. In general, weather had minimal influence on fine-scale temporal deer movements. Therefore, deer in southern latitudes may not be as affected by weather as deer from northern latitudes, which experience more extreme weather

conditions. Thus, deer tend to maintain normal movement patterns regardless of weather conditions, possibly by seeking more favorable habitats.

The public is increasingly concerned with issues related to white-tailed deer management, particularly if any negative biological impacts may result from the management actions. For example, an antler point restriction in Mississippi alleviated unbalanced age structures among males but negatively impacted cohort antler development (Demarais et al. 2005). Additionally, management practices such as selective harvest of males and “high-fencing” (i.e., the enclosure of wildlife behind 2.5-m high fences) have raised concerns related to potential genetic implications of such practices. Selectively removing the largest individuals based on phenotype (Fitzsimmons et al. 1995) or enclosure by impermeable fencing may reduce genetic variability (Hartl et al. 2003).

Several studies found a genetic link between heterozygosity of allozymes and morphometric traits in ungulates. Deer with small antlers were more inbred, based on homozygosity of allozymes, than deer with larger antlers (Smith et al. 1976). Individuals which were more heterozygous had greater antler sizes or points in white-tailed deer (Smith et al. 1983, Scribner et al. 1984, Scribner and Smith 1990, Smith et al. 1991). To determine whether a genetic link to observed antler characteristics was possible, I obtained antler and genetic data from 3 diverse populations of white-tailed deer across their range to test whether antler characteristics were related to heterozygosity.

Most individuals from the 3 study populations were relatively unrelated and heterozygous. It did not appear that deer with similar antler characteristics shared close

common ancestors. However, most deer with antler malformations were more inbred than deer without antler malformations. The few deer with antler malformations may reveal rare cases of close inbreeding. Last, there were not strong relationships between most measures of inbreeding and antler points and score.

Factors such as hunting (Hartl et al. 1995, Harris et al. 2002, Hartl et al. 2003), population size (Ryman et al. 1981), and confinement to fenced enclosures (Hartl et al. 2003) may also affect genetic characteristics of the population. My one enclosed population of white-tailed deer in Oklahoma showed similar levels of heterozygosity to large free-ranging populations from Mississippi and Texas. Selective harvest has also been implicated in influencing genetic properties of hunted populations (Ryman et al. 1981, Hartl et al. 1995, Harris et al. 2002, Coltman et al. 2003, Hartl et al. 2003). If antler quality were related to genetic variability (i.e., heterozygosity), and selective harvest influences genetic variability, then heterozygosity may be expected to differ between Mississippi and the other 2 populations. Based on these data, all populations had similar levels of genetic diversity. Therefore, AR may not result in changes in population level genetic diversity because antler size and heterozygosity were not strongly related. Based on these data, selective harvest programs may improve mean cohort antler size at maturity, but not the genetic characteristics of the population. Thus, selective harvest should focus on removing individuals to maintain proper densities and age structures.

More data is needed to determine how management for white-tailed deer, using selective harvest, can influence antler size and if there are any potential biological

consequences. Modeling is one approach to accomplish this task and may be applicable for predicting when and if selective harvest can cause evolutionary changes (Allendorf et al. 2008). I used stochastic quantitative genetics models (i.e., GENUP; Kinghorn 1992) to evaluate the potential genetic effects of selective harvest on deer antler size. These simulations were based on quantitative genetics theory for transmission of genetic effects between generations. Results came from realizations of genetic change due to the propagation process, and were not dependent on simplifying assumptions usually required to make predictions of genetic change. In addition, I determined the relative contribution of population size, age structure, mating success, and heritability on improving response of antlers to selection. Response to selection was observed through changes in mean population antler size because changes in gene frequency are typically hidden (Falconer and Mackay 1996).

Models developed in Program GENUP provided flexibility in simulating a wide range of scenarios from captive breeding operations to large free-ranging populations. Observed response to selection (i.e., antler points) from captive facilities in Texas (Lockwood et al. 2007) was within the range of model results, indicating models would be useful for predicting response to selection in free-ranging populations. Both empirical and model results revealed similar findings; response to selection will be more rapid and greater in controlled, captive situations. Contrary to findings from captive simulations, selection increased AP by 0.1-0.9 in free-ranging populations even after 20 years of selection. This is because modeled captive populations differed markedly from free-ranging populations for several reasons. First, in captive populations, fewer males were

used for mating and were likely able to sire more offspring because of greater mating success. Second, more variation was observed in antler points in captive populations compared to free-ranging population models, which allows the most superior males to more readily be identified. Third, captive populations also had greater reproductive rates than free-ranging populations, which allowed fewer individuals to be retained for breeding each year. Last, in captive facilities, information (i.e., phenotypes and pedigrees) is available on males and females leading to better mating strategies (e.g., assortative mating). For these reasons, response to selection will be slower, if at all detectable, in free-ranging populations compared to captive populations.

These model results provide information valuable to biologists managing to increase population antler size. Selective harvest in free-ranging populations may be inefficient alone to elicit a response. Selective harvesting should be justified only for controlling population numbers and improving cohort antler size but not for changing the genetic characteristics of free-ranging populations. Careful attention should be paid to harvest strategies, particularly when intense selective harvest causes genetic or evolutionary changes (Coltman et al. 2003, Allendorf et al. 2008). Although phenotypic changes may not be visible, more cryptic genetic changes may be occurring, which warrants observation of genetic variation over time as the population is exposed to selective harvesting. Closed populations require more intense monitoring as gene flow may be limited from surrounding populations; a problem not as evident in large, free-ranging populations where immigration and emigration frequently occur.

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APPENDIX A
WHITE-TAILED DEER (*ODOCOILEUS VIRGINIANUS*) CAPTURED
ON THE SAMUEL ROBERTS NOBLE FOUNDATION
WILDLIFE UNIT FROM 1999-2005

ID	Year	Sex	Age	Fix schedule		Number of relocations
				First	Last	
1	1999	Female	2.5	26 February	30 April	5,456
2	1999	Male	2.5	2 March	6 April	3,208
3	1999	Female	1.5	5 March	3 May	5,459
5	1999	Female	2.5	11 March	13 May	5,458
6	2000	Female	2.5	26 February	19 April	2,790
7	2000	Male	2.5	4 April	12 April	546
8	2001	Female	5.5	25 February	24 April	3,717
9	2001	Male	6.5	5 March	19 May	6,383
10	2001	Female	3.5	6 March	14 May	5,274
11	2001	Male	1.5	7 March	13 May	4,810
12	2001	Female	6.5	8 March	3 May	2,134
13	2002	Male	2.5	15 February	28 March	2,628
14	2002	Male	2.5	15 February	21 March	2,526
15	2002	Female	3.5	25 February	18 April	3,441
16	2002	Female	2.5	17 March	13 May	2,341
17	2002	Male	3.5	20 March	13 May	3,114
18	2003	Female	2.5	3 May	24 June	1,461
20	2003	Female	2.5	1 May	22 June	1,521

ID	Year	Sex	Age	Fix schedule		Number of relocations
				First	Last	
21	2003	Female	3.5	28 May	22 June	506
22	2003	Female	2.5	30 April	26 June	2,732
23	2003	Male	2.5	13 November	20 January	5,798
24	2003	Male	3.5	20 November	8 February	7,160
25	2003	Male	4.5	22 November	6 December	1,316
26	2003	Male	4.5	11 December	13 February	3,931
27	2004	Male	1.5	19 December	7 February	4,250
28	2004	Female	3.5	31 May	9 August	5,320
30	2004	Female	1.5	1 June	7 August	4,671
32	2004	Female	4.5	1 June	12 August	6,150
33	2004	Female	3.5	1 June	10 August	5,566
34	2004	Male	6.5	24 November	17 January	5,000
37	2005	Male	2.5	17 February	15 May	7,945
38	2005	Male	2.5	17 February	9 May	7,486
