

**Mate Choice, Reproductive Success, and How Population Demography
Influences Fawning Season of White-tailed Deer**

by

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A thesis submitted to the Graduate Faculty of
Auburn University
in partial fulfillment of the
requirements for the Degree of
Master of Science

Auburn, Alabama
August 2, 2014

Keywords: White-tailed deer, parentage analysis, reproductive success, mate choice, vaginal
implant transmitter, breeding season, demography

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Abstract

Mate choice of white-tailed deer based on age and body size is poorly understood. I studied a captive population to evaluate mate choice and reproductive success. Age differences between mated pairs did not differ from random pairings and I found no apparent relationship of skeletal size between mated pairs. My results highlight the plasticity of mating success and reveal the mating system of white-tailed deer has evolved to maximize fertility.

Sex ratio and age class may influence timing and duration of the fawning season. I recorded birth date of fawns born within a 174-ha captive facility. The herd was intensively monitored which allowed me to document an earlier shift in fawning following a maturation of age structure. Earlier fawning may be important for neonatal development and survival, especially in areas of the Southeast where coyotes are reducing recruitment. I hypothesize managers can increase neonate development and survival by increasing male age structure.

Acknowledgments

I thank Dr. Steve Ditchkoff for his professional mentorship which enhanced my ability to articulate my results scientifically. Chad Newbolt deserves recognition for dealing with my never-ending requests for supplies and equipment. I thank Dr. Todd Steury for assisting with data analysis and for helping me understand the concept of biological significance. I appreciate Dr. Randy DeYoung for providing critical advice on how to properly analyze microsatellites and how to assign parentage using genetic software. I also thank Dr. Mark Smith for making me a better writer and for advice on how to handle difficult interactions with the general public. I greatly appreciate the sources of funding for this project: the Center for Forest Sustainability at Auburn University, Code Blue Scents/EBSCO Industries, and Record Rack, as well as a large group of individuals who provided private support during the study. To all of my volunteer technicians, especially Clayton Glassey, Hunter Brooks and James Garrett, I am very grateful for your assistance in capturing deer and monitoring transmitters. Without your sacrifice, I would have never been able to collect the enormous amount of data that helped set my project apart from others. Finally, I thank my wife, Jenny Neuman, as well as my family back in Minnesota for supporting my move across the country to become a better wildlife biologist.

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Chapter1: Mate Choice and Reproductive Success of Female White-tailed deer

Abstract

Mate choice based on age and body size is poorly understood among cervids. I used 14 microsatellite DNA loci to reconstruct the pedigree of a captive population of white-tailed deer (*Odocoileus virginianus*) in order to evaluate mate choice and reproductive success. I assigned both dam and sire to 87 known-age litters over 6 years. Age differences between mated pairs did not differ from random pairings and I found no apparent relationship of skeletal size between pairs. My results highlight the plasticity of mating success for white-tailed deer and I speculate their mating system has evolved to maximize fertility. My investigation was the first to explore mated pairs with such a high proportion of candidate parents sampled and the first to incorporate vaginal implant transmitters to validate genetic sampling techniques. This knowledge could help local and regional wildlife managers comprehend the unpredictability of mating success in white-tailed deer.

Introduction

In polygynous ungulates, most species have evolved a mating system that creates sexual dimorphism where the adult male is larger than the adult female (Isaac 2005). The most widely accepted theory for the cause of sexual dimorphism is sexual selection and differential parental investment (Andersson 1994). In most mammals, female reproductive success is limited by their ability to raise offspring; whereas males are limited by the number of effective matings they can acquire (Trivers 1972). Male-male competition leads to variance in reproductive success between the sexes. In natural populations with balanced sex ratios, female reproductive success is rather fixed, but male reproductive success is highly variable (Bateman 1948). Whenever

reproductive success is apportioned to a greater segment of the male population, sexual selection cannot act as strongly and sexual dimorphism will be less pronounced (Isaac 2005).

Male mammals are only guaranteed paternity if they monopolize breeding with a female or group of females. Emlen and Oring (1977) described the relationship of ecological constraints to the degree of monopolization that occurs among species. Open habitats often allow males to monopolize multiple females, such as with polygynous red deer (*Cervus elaphus*), where males gather and defend harems in open meadows (Clutton-Brock et al. 1982). The mating system of white-tailed deer (*Odocoileus virginianus*) is also generally characterized as polygynous, with recent evidence of female promiscuity coming from observations of multiple paternity (DeYoung et al. 2002, Sorin 2004; DeYoung et al. 2009). Male white-tailed deer, however, do not typically monopolize >1 female at a time (Sorin 2004; DeYoung et al. 2009). Rather, males follow and defend a single female for a period up to 72 hours (Hirth 1977). Although habitats vary greatly within the range of white-tailed deer, they tend to be found near areas of thick vegetative cover which may explain why males only monopolize one female at a time (DeYoung and Miller 2011).

Although white-tailed deer are the most studied and abundant ungulate species in North America, few studies have examined their mating success using genetic techniques. Of the few studies that have been conducted, emphasis was placed on the physical attributes of males such as age and body size (Sorin 2004; DeYoung et al. 2009; Jones et al. 2011). There has, however, been extensive effort using number of fawns born to quantify the attributes of successful females by age, nutritional status, and body size (Haugen 1975; Kie and White 1985; Ozoga and Verme 1986a, 1986b; Ozoga 1987; Mech and McRoberts 1990; Nixon and Etter 1995; DelGuidice et al. 2007). The results of each study differ by region and nutritional availability, but the trend is

similar across areas; fawns rarely breed, yearlings usually have 1 fawn, and 2.5+ year olds produce more twins than younger age classes. These reproductive parameters are vital for models that estimate deer populations which are important for making future harvest recommendations (Hansen 2011).

While individual male and female physical attributes are certainly important when trying to understand breeding success of white-tailed deer, combined attributes between mated pairs have received scant attention in the literature. Ozoga and Verme (1985) documented age relationships between experimentally manipulated male populations and females. When mature males were absent from the population, yearling males mated with females of all ages and there were no short term changes to female productivity. They also observed less ritualized breeding behavior, such as antler rubbing and ground scraping by yearling males which they attributed to a lack of social structure. Sorin (2004) reported 1.5 year old males were only able to secure breeding opportunities with young (≤ 2.5 year old) females while mature males concentrated efforts on older females. Unfortunately, her results were limited to an examination of age of mated pairs and were not able to provide information about how female or male body size influenced pairings.

Although speculation abounds, there is uncertainty concerning whether female mate choice or male-male competition drives the mating system of white-tailed deer. Females only mate with males during their estrous cycle, but males have been known to act aggressively toward females that were not allowing them to breed which brings into question if the female is choosing or if she is breeding for self-preservation (Haugen 1959). It is generally believed that in cases where intra-male competition occurs, the male is eager to mate with any receptive female, without discrimination, whereas the female chooses the male (Trivers 1972; Emlen and

Oring 1977). However, Berger (1989) noted that when males can only secure a limited number of matings and females exhibit reliable cues to their reproductive potential, males were more selective. Margulis (1993) found evidence for selection bias among males by observing that male mule deer (*O. hemionus*) chased females that did not recruit offspring during the current year more than females with fawns present. Sorin (2004) suggested mature males concentrated efforts on older females because they produced more twins than yearling females. However, the role of female physical attributes on male mate selection has yet to be firmly established.

In this study, I monitored a captive population of white-tailed deer exhibiting natural breeding behavior and evaluated mate choice using offspring parentage assignments. My goal was to examine relationships between mated pairs with regards to age and body size, and specifically investigate the role of female selectivity during the mating process. I predicted age and body size would be positively correlated between mated pairs as individuals concurrently seek to maximize fitness (Sorin 2004, Berger 1989). Another goal was to observe how age and body size influence recruitment. I predicted that older, larger females would recruit more offspring than younger, smaller females (Ozoga and Verme 1986b; Nixon and Etter 1995). I predicted that younger males that successfully bred were larger than similar-aged bucks that did not breed in terms of their age adjusted body size (Jones et al. 2011).

Materials and Methods

Study Area

The white-tailed deer in this investigation resided in the 174-hectare Auburn Captive Facility (ACF) located in Camp Hill, Alabama, USA. The population consisted of deer that were in the area at the time the fence was constructed in 2007, and their descendants. The perimeter of the ACF was bordered by a 2.6-meter deer-proof fence which allowed the study of individuals throughout their lifetime. Except for dispersal, deer were allowed to move freely and behave

naturally. Deer were fed 18% protein pellets (“Deer Feed,” SouthFresh Feeds, Demopolis, AL) ad libitum year round using 3 free choice feeders. Their diet was supplemented by 4 timed corn feeders providing approximately 2 kg/day of corn during fall and winter which helped attract deer for capture.

The two main cover types inside the ACF were open hayfields (40%) maintained for hay production and mixed forest (60%) managed for wildlife habitat using prescribed fire. The predominant grass species found inside the ACF was bermuda grass (*Cynodon* sp.). Other grasses present included fescue (*Festuca* sp.), big bluestem (*Andropogon* sp.), Johnson grass (*Sorghum* sp.), dallisgrass (*Paspalum* sp.), and bahia grass (*Paspalum* sp.). The mixed forest consisted of 70 % hardwoods which included various oak (*Quercus* spp.), hickory (*Carya* spp.), and maple (*Acer* spp.) species and 20 % conifer which consisted of loblolly pine (*Pinus taeda*). The remaining 10 % of mixed forest was made up of naturally regenerated thickets of *Rubus* spp., sweetgum (*Liquidambar styraciflua*), eastern red cedar (*Juniperus virginiana*) and Chinese privet (*Ligustrum sinense*).

The general habitat among the wooded areas included a thick closed canopy with little understory growth. Locations where sunlight could penetrate the canopy along forest edges and creek bottoms contained dense understory growth. A stable water source was available to deer from 2 creeks that flowed through the property. Elevation ranged from 190 to 225 meters above sea level. The climate in this region of East-Central Alabama was moderately warm with mean high temperatures of 32.5 °C in July and mean low temperatures of -0.5°C in January. Average annual precipitation in the area was approximately 131 cm.

Capture and Data Collection

Adult (≥ 6 months old) deer were captured using either a 0.8 ha capture facility or cartridge fired dart guns equipped with night vision scopes. Chemical immobilization occurred

with an intramuscular injection of Telazol® (Fort Dodge Animal Health, Fort Dodge, Iowa; 125mg/ml given at a rate of 4.5 mg/kg) and xylazine (Lloyd Laboratories, Shenandoah, Iowa; 100mg/ml given at a rate of 2.2 mg/kg) followed by reversal with Tolazine® (Lloyd Laboratories, Shenandoah, Iowa; 100mg/ml given at a rate of 6.6 mg/kg; Miller et al. 2004). The capture facility allowed for the capture of multiple individuals with one trapping effort. It consisted of a modified box trap at the end of a 0.8 ha deer proof fence. Deer entered the trap through an open gate and once the group was calmly feeding, the gate was closed behind them. The layout of the fence funneled deer into the box trap, which was closed using a remote gate. Sorting boxes were positioned at one end of the box trap to facilitate chemical immobilization. Darting was conducted from tree stands over automated feeders from mid-September to early June. Dart guns used telemetry darts (2.0 cc, type C, Pseudart Inc, Williamsport, PA) to locate immobilized deer (Kilpatrick et al. 1996).

Measurements of adult deer included head, body, hind foot, and chest. Chest girth was measured immediately posterior to the front legs, hind foot length was measured from the tip of the hoof to the posterior end of the tuber calcis (tarsal), and body length was measured from the tip of the nose to the base of the tail dorsally along the head and spine (Ditchkoff et al. 2001). Deer were aged using tooth replacement and wear method (Severinghaus 1949). Although this method has come under recent scrutiny (Gee et al. 2002), I minimized potential errors by limiting aging assignments to 3 biologist who were familiar with tooth wear patterns of deer in the facility. Also, the majority (72%) of age assignments occurred when deer were <20 months old and had not lost their tricuspid pre-molars. Deer initially captured and aged ≤ 1.5 years old were considered known-age for my study. Thus, a deer captured at 1.5 years old in 2008, was considered a known-aged 4.5 year old in 2011. All deer not captured previously were ear tagged

and freeze branded with unique numbers in order to identify individuals. Tissue samples were collected via 1-cm ear notch and stored at -78°C until further analysis.

Fawns were captured using Vaginal Implant Transmitters (M3930, Advanced Telemetry Systems, Isanti, MN; hereafter VITs) following procedures described by Saalfeld and Ditchkoff (2007). VITs were placed in females captured from late February to early June. I monitored VITs every 6 hours during the fawning season to determine if the transmitter was expelled. Hand held telemetry was used to determine the location of the birthing site using methods of Carstensen et al. (2003). A thermal imaging camera (Raytheon Palm IR 250D, Waltham, MA) was used to aid in locating fawns not found at the birth site. All capture and handling procedures were in accordance with protocols approved by the Auburn University Institutional Animal Care and Use Committee (PRN numbers: 2008-1417, 2008-1421, 2010-1785, 2011-1971, and 2013-2372) and were in compliance with guidelines adopted by the American Society of Mammalogists Animal Care and Use Committee (Sikes et al. 2011).

Population Monitoring

The relatively large area of the ACF combined with rolling terrain did not allow me to view all animals at one time; therefore I used a combination of methods to estimate population demographics. I used bi-yearly camera surveys at sites baited with shelled corn and along trails (McCoy et al. 2011). Ear tags, freeze brands, and unique antler configurations allowed me to identify individuals and estimate abundance, sex ratio, and age structure of the population. I applied mark-recapture techniques to estimate the proportion of adults sampled for parentage assignments (Pollock et al. 1990; Karanth and Nichols 1998). Marked individuals were not fitted with mortality detectors which created some uncertainty regarding prolonged absence of some individuals from the camera surveys. I considered marked individuals not seen by camera or

field observations for 2 years as possibly deceased and removed them from the pool of candidate parents. I used camera survey data in conjunction with current capture and mortality records to reconstruct the total population for each year and generate final estimates of demographics.

The goal was to maintain a population of ≤ 120 adult deer during the study. The population was not hunted, so annual population regulation occurred via natural mortality, capture related mortalities, and selective removal of fawns. I captured 10 individuals (5 female, 5 male) < 1 years of age at random and released them outside the enclosure each trapping season beginning in September 2010. Deer were removed in this manner to maintain a relatively even distribution of individuals among cohorts, and prevent negative social effects known to occur in crowded populations of white-tailed deer (Ozoga and Verme 1982).

Microsatellite Analysis

Microsatellite markers were scored by DNA Solutions (Oklahoma City, Oklahoma) using the panel first described by Anderson et al. (2002). I estimated allelic richness (El Mousadik and Petit 1996), gene diversity (Nei 1973), and F_{is} (Weir and Cockerham 1984) using FSTAT (Goudet 1995, 2001). The program also tested Hardy-Weinberg equilibrium (1,000 permutations of alleles among individuals) and linkage disequilibrium among loci (10,000 permutations of genotypes). A Bonferroni correction was used in order to correct for multiple comparisons (Rice 1989).

I defined reproductive success as the successful birth of offspring, or the siring of a fawn by males. My sample did not include fetuses or fawns that were born and died prior to me being able to capture them and collect a tissue sample. The six years of reproductive success data were divided into yearly offspring cohorts, meaning I compiled lists of candidate parents separately for each year offspring were born (2008-2013). Parentage assignments were made using the

likelihood based approach in CERVUS 3.0 (Kalinowski et al. 2007). For each year I entered population demographics into CERVUS which included candidate parents, offspring, percentage of sampled individuals and typing error rates. Simulations provided critical values for the Delta statistic which CERVUS used when assigning parentage. Typing error rates were calculated in CERVUS using known mother-offspring pairings from VITs. Accuracy of CERVUS assignments was calculated by including all candidate mothers and comparing results to known mother-offspring pairings from VITs. Male and female fawns alive during the breeding season were included as candidate parents because several studies have documented that fawns are capable of producing young (Schultz and Johnson 1992, Peles et al. 2000). Parentage assignments were ordered by delta LOD and assignments were selected based on trio confidence, which incorporated both parents' genotypes in the likelihood based algorithm (Kalinowski et al. 2007). To be conservative, only trios with 95% confidence were included in the final analysis of reproductive success.

Statistical Analysis

I used data from 6 years (2008 to 2013) of reproductive success inside the ACF to determine physical attributes between mated pairs. For female reproductive success, I used a generalized mixed effects regression with Poisson distribution in R (R core development team, version 15.3 accessed 10 December 2013). The number of fawns recruited by females was compared to age and body size of a random group of females, including a random effect of individual because some females were measured several times throughout their lifetime. Year was included as a random effect to account for unknown differences in nutritional availability between years.

Skeletal growth patterns of white-tailed deer differ between the sexes, so our variable grouping of individuals by age reflects this difference (Ditchkoff et al. 1997, Ditchkoff 2011). Male skeletal body sizes were grouped into six categories: fawns, 1.5, 2.5, 3.5, 4.5, and 5.5+ years old. Once female white-tailed deer reach 2.5 years of age, most are close to their maximum body size and can put more resources toward reproduction rather than individual growth. As a result, females were only grouped into three categories: fawns, 1.5, and 2.5+ years old. Age and body size relationships between mated pairs were analyzed using linear regression in R (R core development team, version 15.3 accessed 15 December 2013).

I was unable to capture every adult in the population every year, which left gaps in the dataset regarding body size of one or both parents in a mated pair. In order to examine size relationships in years when the dam or sire(s) were not measured, I used percentiles. I did this in order to include information I had gathered about individuals throughout their lifetime, but may not have captured them in the year they produced a fawn. I calculated percentiles by pooling all measurements across all years and grouped them by age. I assigned percentile scores to individuals with ≥ 2 years of skeletal body measurements. For instance, if a male was initially captured at 1.5 years old and measured 258 cm (body, hind foot, and chest combined), I compared his skeletal growth to all other 1.5 year olds measured. Assume this individual ranked 12th out of 36 individuals measured at age 1.5, which would put him in the 68.4 percentile. If that male were subsequently captured at age 3.5 and 5.5, I calculated the mean percentile score of his lifetime body size and used that number in my correlation of body size if he sired offspring at 4.5 years old. Skeletal body sizes were normally distributed around the mean, meaning I felt confident our percentile assignments did not inflate or deflate individual body rankings when compared to similar aged males.

Results

Demography

Population estimating methods indicated that minimum annual herd size ranged from 69 to 122 individuals from 2008 to 2013 (Table 1.1). Adult sex ratio gradually shifted over the course of the study from a female majority in 2008 to a male majority in 2012. Approximately 90% of adult deer have been captured and marked. The proportion of known-age animals in the population has increased from 50.7% in 2008 to 81.8% in 2013. Mean adult (>0.5 years old) male age increased from 1.42 in 2008 to 3.92 in 2013, while mean adult female age increased from 2.14 in 2008 to 4.17 in 2013. Initial density was 0.4 deer/ha in 2007 and peaked in 2011 at 0.7 deer/ha. Initial sex ratio was 1:2 M:F, which gradually shifted toward parity with an estimated ratio of 1:0.9 M:F in 2013.

Genotyping

DNA Solutions, Inc. genotyped 224 deer captured from October 2007 to July 2013. Forty-four of 224 (19.6 %) deer were first captured as neonates, and 180 of 224 (80.4 %) were captured when ≥ 6 months old. DNA Solutions, Inc. originally genotyped 14 loci, but 3 loci (Q, D, and P) deviated significantly from Hardy-Weinberg equilibrium and were subsequently excluded from parentage analysis (Table 1.2). Allelic richness ranged from 4 to 16 alleles per locus ($\bar{x} = 9.93$). Equilibrium tests revealed linkage disequilibrium at 9 of 91 pairwise combinations of loci (Cervid and BL25, L and O, L and P, BM6506 and D, N and BM6438, BM6438 and Q, O and S, D and OAR, and P and S). All remaining loci were retained despite observed genotypic disequilibrium as linkages at this level are not likely to alter parentage assignments (Sorin 2004). The proportion of candidate parents sampled varied from 50 % in 2008 to 90 % from 2009 to 2012 (Table 1.3). The 90 % sampled rate from 2009 to 2012 was a

conservative estimate based on our population monitoring methods. In 2013, sampled percentage was set to 80 because at least ten individuals born in 2012 that remained uncaptured when data were analyzed.

Parentage

I assigned both sire and dam to 87 known-age litters at the 95% confidence level. Twenty-four of 87 (27.6 %) assigned dams were known-age whereas 30 of 87 (34.5 %) assigned sires were known-age individuals. CERVUS correctly assigned maternity for 35 of 37 (94.6 % accuracy) offspring collected using known mothers by way of VITs. The comparison of age differences among breeding pairs to a random distribution of available pairings yielded no difference ($\chi^2 = 20.69$, $d.f. = 18$, $P = 0.295$; Fig. 1.1). The general relationship between dam and sire age did not differ from what would be expected if random mating had occurred ($t = 1.017$, $d.f. = 84$, $P = 0.312$; Fig. 1.2). Collectively, male fawns and yearlings mated with 13 females, of which, 6 females were ≥ 3.5 years old. One yearling male bred with a 7.5 year old female. Male reproductive success was highly variable and changed according to available male age structure. In 2008, 7 of 14 (50 %) mated pairs included 1.5 year old males, whereas only 1 of 6 (17 %) mated pairs included a 1.5 year old male in 2013 when male age structure was more mature. Multiple paternity occurred in 10 of 27 (37 %) sets of twins. Nine of 10 cases of multiple paternity involved dissimilar aged males, and the one case of same-aged males occurred between dissimilar sized males.

Herd reconstruction using assigned parentage allowed me to compute minimum recruitment values for females. As expected, reproductive success for females ≥ 2.5 years old did not vary as much as with males. Physically mature females (≥ 2.5 years old) for which recruitment data were available recruited $1.22 (\pm 0.073 SE, n = 54)$ offspring into the fall

population. Adolescent females (1.5 years old) for which recruitment data were available recruited $0.76 (\pm 0.077, n = 13)$. I documented 9 fawns that recruit offspring into the fall population, and they each recruited one individual. Females ≤ 1.5 years old failed to recruit more than 1 offspring during the study period. Two different females each recruited one litter of triplets during the study period. Mean age for females that recruited 2 or more individuals into the fall population was $4.44 (\pm 0.359, n = 16)$ years old.

Generalized mixed model regression analysis indicated that for every 10 cm increase in skeletal size, females recruited 1.35 (1.07-1.74; 95% C.L., $P = 0.036$) times as many fawns. Additionally, I found no relationship ($t = 1.48, d.f. = 16, P = 0.158$) between skeletal sizes of 18 mating pairs for which we had measurements of both parents (Fig 1.3). Using lifetime body percentile as a surrogate for body size allowed me to compare size relationships for 82 pairs, which also resulted in no relationship ($t = 0.487, d.f. = 81, P = 0.628$; Fig. 1.4).

Discussion

My findings do not support my original hypothesis that white-tailed deer selectively choose mates of similar age or body characteristics as themselves. Sorin (2004) found that yearling males only mated with young females (≤ 2.5 years old), but I found yearling males reproduced with older females (> 2.5 years old) as well. Sorin (2004) stated that experienced females might not tolerate advances by young males, but of the 10, 1.5 year old males known to have sired offspring during our study, 4 mated with females ≥ 3.5 years old. My results show that tolerance of advances made by young males occurred, with evidence of an extreme example in 2008 when a 1.5 year old male mated with a 7.5 year old female. Other studies described similar results regarding young males breeding. Ozoga and Verme (1985) indicated 1.5 year old males gained mating opportunities with females of all ages, although no older males were competing

against them within that experimental population. DeYoung et al. (2009) reported physically immature males (1.5 and 2.5 years old) collectively fathered 30-33% of offspring in 3 separate populations, even when mature males were present. They reasoned that the overall spatial dispersion of females within populations combined with temporal breeding synchrony would limit the number of estrous females an individual male could locate and breed. This in turn allowed mating opportunities for males of all age classes.

Most studies of reproductive success in white-tailed deer have been presented with regards to age, but it is uncertain if deer are capable of perceiving age of potential mates or if they simply use physical characteristics such as body size. If a situation arises where a male must choose between 2 females in estrus, Berger (1989) suggested the male should choose the larger female, thereby increasing his odds of siring more offspring than if he mated with the smaller female. Although not significant, I noticed a trend where female skeletal size was associated with a female's ability to recruit offspring. The inability of our data to document productivity bias by skeletal size could have been an artifact of our sampling of litters, which mostly (80.4%) consisted of recruited individuals rather than neonates. I did not document a body size preference but instead found that mating occurred between a wide range of male and female body sizes. This finding suggests that males may not be choosy when mating. Rather they may just pursue females based on chemical signals regarding receptiveness (Murphy et al. 1994) rather than physical attributes.

The wide range of ages and body sizes I documented between mated pairs highlights the plasticity of mate choice in white-tailed deer. There is an inherent choice a female must make when she is being pursued by a lesser quality mate: should she breed during her first estrous cycle or wait until a larger, more dominant buck arrives? This decision is important because late

breeding may put a female's offspring at a reproductive disadvantage later in life due to retarded development and later age of puberty of offspring (Zwank and Zeno 1986; Gray et al. 2002). Additionally, females who breed during the peak breeding season may have reduced predation on their offspring due to the predator swamping effect (Whittaker and Lindzey 1999). Our results suggest females of all ages and sizes will mate with a younger, smaller male which supports a female choosing to mate instead of holding out for a better quality male. Similar results were reported by Haugen (1959), when mature females outside of estrus refused to accept advances made by a young male inside a small pen by fighting him off with their front feet. On the day the females entered estrus; however, their demeanor changed and they stood quietly and calmly until serviced by the male (Haugen 1959). Although speculative, I hypothesize that choosiness during mate selection changes as a female approaches the end of her period of receptivity. Females that do not tolerate advances from young males (Sorin 2004) may not be in estrus or may only be in the beginning stages of estrus. White-tailed deer have evolved a mating system that allows nearly all reproductive-aged females to be fertilized (Verme and Ullrey 1984; DelGuidice et al. 2007), which may explain why seemingly poor quality mates of both sexes successfully breed.

The mate choice decision is confounded by the fact that population demographics play a central role in the dynamics of choice simply through availability. When there are comparatively fewer mature males present, females may be more apt to breed with younger males simply because there are not enough mature males to service each female (Ozoga and Verme 1985; DeYoung et al. 2009). I observed that as the male age structure matured, the proportion of breeding by 1.5 year old males decreased. This suggests that young males may change behavioral breeding strategies based on competition from other males. Male breeding success

may not actually be random, but it appeared random in our analysis, possibly as a result of changing demographics. When the enclosure was first constructed there was a young male age structure with the oldest males 3.5 years old. In 2013, however, one male had reached 8.5 years of age, which made any comparisons between years problematic. Experience may also factor into the pair-bonding process because young males may not adequately service females in their first attempt to copulate, which may allow enough time for another male to find the pair and displace the subdominant male. The displacement of individuals in a tending bond mating system may occur more often when more mature males are cruising the landscape in search of receptive females, but more research needs to be conducted to confirm this speculation.

I found no evidence that males were able to detect differences in female quality based on physical attributes, but evidence suggests males may use other cues to assess female quality (Berger 1989). Margulis (1993) suggested the presence or absence of last year's fawns may influence which females a male rocky mountain mule deer (*O. hemionus hemionus*) will chase. Reproductive expenditures such as gestation and lactation put a strain on the body of females that may lead to reduced success in successive years, also known as alternate-year reproductive success (Mundinger 1981). In years where nutrition is inadequate, females will not allocate resources to their fawns in lieu of maintaining their body mass (Therrien et al. 2007). This is a strategy that helps facilitate lifetime reproductive success by increasing the female's chance of survival at the cost of losing offspring during the current year. The nutritional demands of reproduction/lactation may mirror those associated with nutritional restriction due to climate or food shortages. According to Pekins et al. (1998), the total energetic costs of gestation are 16.4% greater than the requirements for non-pregnant does, so pregnant does cannot afford to put resources toward body growth. Lactation is even more demanding as it requires 1.7 times more

energy than gestation (National Research Council 2007) and reduced fecundity can occur after successfully weaning offspring (Clutton-Brock et al. 1989; Therrien et al. 2007). This has been found in other ungulate species such as bighorn sheep (*Ovis canadensis*) where females reduced their reproductive effort when population density increased and if they had weaned a lamb the previous year (Martin and Festa-Bianchet 2010). I did not observe a male bias against females that had recruited fawns the previous year, but our results may differ from wild populations because our population had access to supplemental feed.

Our results support previous studies (Verme 1969; Haugen 1975; Folk and Klimstra 1991) that found an influence of skeletal size, age, and nutritional status on reproductive success in adult, female white-tailed deer. Although quality of offspring is certainly important, most data available for white-tailed deer are reported by quantity of offspring produced by female age class, which is correlated with body size. Body size varies by region and nutritional availability as deer from the fertile soils of the Midwest tend to have larger bodies than deer in the Southeast, and their fetal rates reflect this difference (Ditchkoff 2011). Verme (1969) compared reproductive patterns of white-tailed deer related to a nutritional plane and found that deer on a low quality diet had less fawns per doe than those on a high quality diet. The effects of body size on reproductive potential tend to be more pronounced in younger age classes. Rhodes et al. (1985) indicated that fawns in South Carolina had an average of 1.06 fetuses, yearlings had an average of 1.56 fetuses, and 2.5 year old does had an average of 1.73 fetuses. Beyond 2.5 years old, the combined litter size was 1.76 for all older age classes. The same trend was found in a study on the productivity of female deer in Illinois in which fawns had 1.00 fetuses, yearlings had 1.76, 2.5 year old does had 1.90, and combined older age classes had 1.93 fetuses (Rosenberry and Klimstra 1970). Verme and Ullrey (1984) found that female fawns must reach

a critical weight of 36 kg in order to reach puberty and ovulate, which occurred in at least 9 of 63 (14%) female fawns on our study site. Similarly, our results demonstrated that a younger, smaller body size correlates with less fawn recruitment than older, larger deer: but only to a certain age.

Although our observations of mated pairs were derived with small sample sizes from only one population, similar tendencies would be expected across the white-tailed deer's range. I concentrated efforts inside a 174-ha high fence enclosure which minimized losses of reproductive aged females due to emigration and hunting mortality, and also allowed deer to be intensively monitored throughout their lifetime. Multi-year reproductive success is difficult to estimate in the wild because white-tailed deer are an inherently cryptic species and yearlings can disperse long distances (>50 km) from their natal range (Long et al. 2005). Because of the closed-nature of the system, I was able to collect detailed data from most individuals in the population, enabling me to examine factors that are extremely difficult in free-range settings. Mate choice was difficult for early researchers to evaluate because adequate genetic techniques were unavailable or mate choice was limited by small enclosure size and number of available mates. For example, using behavioral observations, Hirth (1977) was only able to record 4 copulations over 3 years. Although our facility was only 174 ha in size, and some of the spatial attributes of the population were compromised (e.g., the size of the facility was less than the typical home range of white-tailed deer, closed population), I feel my data are representative of behaviors and mate choices found in a free-range setting. Caution should be used when interpreting body percentiles because they were calculated using measurements pooled across all years. Even though supplemental protein was provided ad libitum throughout the entirety of the study, availability of natural forage from climactic factors could have affected body growth

(Ozoga and Verme 1982). I did not determine if there was an influence of climatic factors on body size because of small sample sizes by age class across years.

Additional studies focusing on the reproductive success of white-tailed deer might incorporate individual behavioral variables, or monitor fine-scale movements of both sexes in order to get a better understanding of how young, physically immature males obtain breeding opportunities, even in the presence of larger more mature males. More research also needs to be conducted on how female mate choice changes over the duration of the estrous cycle in order to maximize fertilization. Employing VITs in a greater proportion of the herd would increase sample size and further validate typing error rates, because more offspring would have at least one known parent. Currently, there is no mechanism other than behavioral observations that can identify males that bred females but were unable to conceive offspring. Future research on reproductive success of free-ranging deer populations with similar proportions sampled as this study would further our understanding of mate-choice in this cryptic species as well as help validate our results.

Acknowledgments

This study was supported by the Alabama Agriculture Experiment Station, Center for Forest Sustainability, and School of Forestry and Wildlife Sciences, Auburn University. I thank V. Jackson for maintaining feeders and habitat within our study site. I appreciate the assistance of many undergraduate volunteer technicians from the School of Forestry and Wildlife Sciences at Auburn University for helping me monitor transmitters and assist in data collection, most notably C. Glassey, J. Garrett, and J. Brooks. Additional thanks to M. Smith and T. Steury for reviewing my manuscript.

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Table 1.1 – Known white-tailed deer breeding populations by sex, age class, and cohort birth year from 2008-2013, Auburn Captive Facility, Camp Hill AL.

Age	2008	2009	2010	2011	2012	2013
Total popln. ^a	69 (35 ^b)	84 (51 ^b)	98 (63 ^b)	122 (90 ^b)	114 (89 ^b)	110 (90 ^b)
Males	25 (15)	40 (29)	48 (34)	62 (50)	64 (53)	53 (45)
0.5	11 (9)	16 (15)	14 (11)	21 (21)	13 (13)	8 (8)
1.5	8 (6)	10 (8)	13 (12)	11 (8)	12 (12)	9 (9)
2.5	3 (0)	8 (6)	9 (7)	12 (11)	11 (8)	6 (6)
3.5	3 (0)	3 (0)	6 (4)	8 (6)	11 (10)	9 (6)
4.5	0	3 (0)	3 (0)	6 (4)	8 (6)	8 (8)
5.5	0	0	3 (0)	2 (0)	6 (4)	7 (5)
6.5	0	0	0	2 (0)	2 (0)	4 (3)
7.5	0	0	0	0	1 (0)	1 (0)
8.5	0	0	0	0	0	1 (0)
Females	44 (20)	44 (22)	50 (29)	60 (40)	50 (36)	48 (36)
0.5	16 (11)	7 (6)	13 (10)	12 (12)	9 (9)	6 (6)
1.5	7 (6)	14 (9)	5 (4)	13 (10)	10 (10)	9 (9)
2.5	8 (3)	5 (4)	13 (8)	5 (4)	8 (5)	8 (8)
3.5	7 (0)	7 (3)	5 (4)	12 (7)	3 (3)	5 (2)

Table 1.1 – Continued

Age	2008	2009	2010	2011	2012	2013
4.5	4 (0)	5 (0)	6 (3)	5 (4)	9 (4)	3 (3)
5.5	1 (0)	4 (0)	4 (0)	6 (3)	4 (3)	8 (4)
6.5	0	1 (0)	2 (0)	3 (0)	5 (2)	4 (3)
7.5	1 (0)	0	1 (0)	2 (0)	1 (0)	3 (1)
8.5	0	1 (0)	0	1 (0)	1 (0)	1 (0)
9.5	0	0	1 (0)	0	0	1 (0)
10.5	0	0	0	1 (0)	0	0
Sex Ratio						
(M:F) ^c	1:2.0	1:1.5	1:1.1	1:1.2	1:0.8	1:0.9

^a Abundances estimated using combination of camera surveys, field observations, capture of live animals, and recovery of deceased animals. All estimating methods indicated $\geq 90\%$ of animals in breeding populations were marked during the study yielding largely known population sizes.

^b Number of individuals initially captured at ≤ 2.5 years old.

^c For animals >0.5 years old.

Table 1.2 – Population genetics information (individual locus allelic richness, gene diversity, F_{IS} , and Hardy-Weinberg probabilities) for white-tailed deer from 2008-2013 at Auburn Captive Facility, Camp Hill, AL.

Locus	Samples	Alleles	Gene diversity	F_{IS}	P^a
Cervid	224	14	0.879	-0.026	0.891
L	223	9	0.776	0.005	0.469
BM6506	224	12	0.890	-0.028	0.907
N	224	13	0.874	0.040	0.071
INRA01	224	5	0.303	-0.090	0.975
BM6438	224	9	0.820	0.026	0.215
O	224	8	0.699	-0.047	0.912
BL25	224	5	0.516	0.083	0.044
K	224	4	0.150	-0.012	0.686
Q ^b	223	14	0.836	0.115	0.001
D ^b	223	10	0.764	0.184	0.001
OAR	224	12	0.826	-0.010	0.673
P ^b	221	8	0.811	0.191	0.001
S	224	16	0.895	-0.018	0.806

^a Indicative adjusted nominal level (5%) was 0.004.

^b Loci excluded from parentage analysis due to departures from Hardy-Weinberg equilibrium.

Table 1.3 – Inputs for yearly cohort simulations of white-tailed deer parentage analysis using CERVUS 3.0 from 2008-2013 at Auburn Captive Facility, Camp Hill, AL.

Year	2008	2009	2010	2011	2012	2013
Offspring	10,000	10,000	10,000	10,000	10,000	10,000
Candidate Mothers	44 (0.5 ^a)	44 (0.9)	50 (0.9)	60 (0.9)	50 (0.9)	48 (0.8)
Candidate Fathers	25 (0.5 ^a)	40 (0.9)	48 (0.9)	62 (0.9)	64 (0.9)	53 (0.8)
Proportion Loci Typed ^b	0.9997	0.9997	0.9997	0.9997	0.9997	0.9997
Proportion Loci Mistyped ^c	0.014	0.014	0.014	0.014	0.014	0.014
Minimum Loci Typed	10	10	10	10	10	10

^a Proportion sampled. Estimated using camera surveys, field observations, capture of live animals, and recovery of deceased animals.

^b Reported in allele frequency analysis in CERVUS 3.0.

^c Calculated using known parent-offspring mismatching rates with offspring collected by way of VITs.

Figure 1.1 – Observed age differences between dams and sires from 2008-2013, and random age differences assuming the occurrence of random mating, Auburn Captive Facility, Camp Hill, AL.

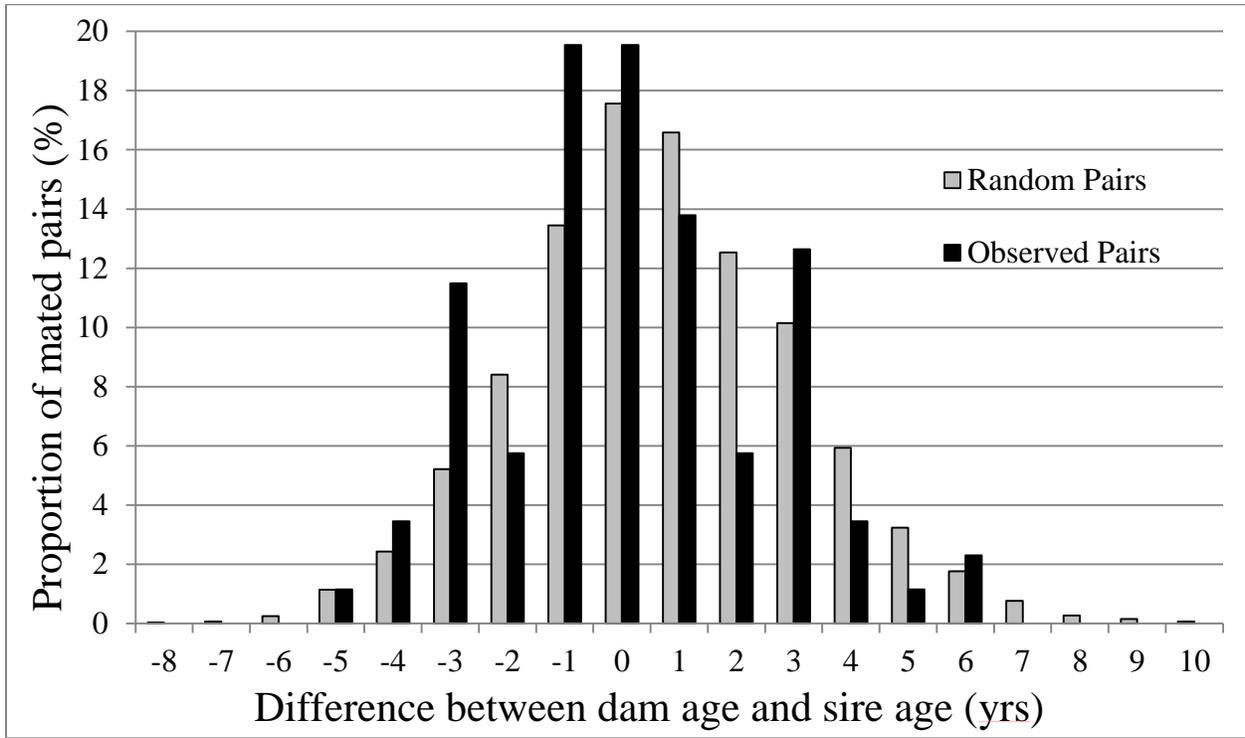


Figure 1.2 – Range-graded dot representation of age relationships between mated pairs of white-tailed deer from 2008-2013, Auburn Captive Facility, Camp Hill, AL.



Figure 1.3 – Size comparison of 18 mated pairs of white-tailed deer for which measurements were available for both parents from 2008-2013, Auburn Captive Facility, Camp Hill, AL.

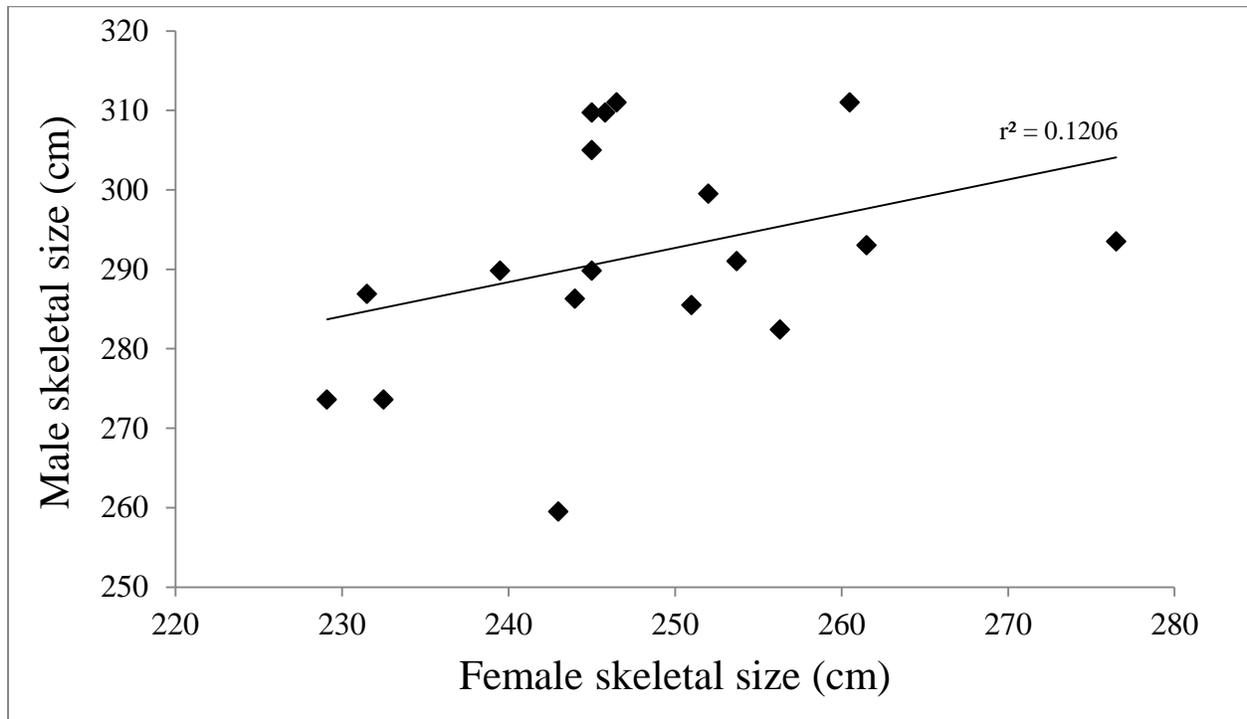
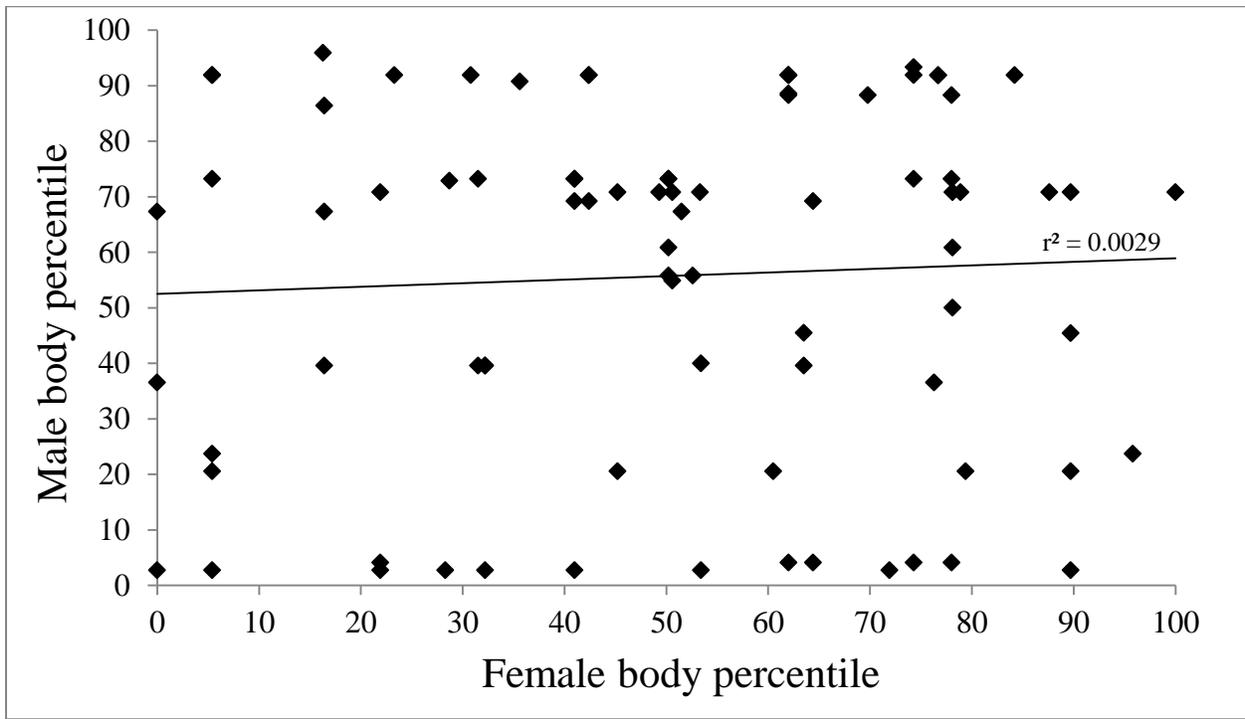


Figure 1.4 – Body percentile comparison between mated pairs of white-tailed deer from 2008-2013, Auburn Captive Facility, Camp Hill, AL.



Chapter 2: How Population Demography Influences Fawning Season of White-tailed Deer

Abstract

Although white-tailed deer (*Odocoileus virginianus*) are one of the most abundant and studied ungulates in North America, few studies of how population demography affects the fawning season have appeared to date. Age structure and adult sex ratio of a population may influence the timing and duration of the fawning season. From 2010 to 2013, I used Vaginal Implant Transmitters (VITs) to record the birth date of fawns born from native Alabama deer enclosed within a 174-ha captive facility to elucidate how population demography affects fawning season. The deer herd was intensively monitored which permitted me to document an earlier shift in fawning season as male age structure increased from a mean of 2.74 years old in 2010 to 3.92 years old in 2013. Prior to the shift, the mean fawning date was 12 August, and after a maturation of male age structure, the mean fawning date was 30 July. Earlier fawning may be important for neonatal survival, especially in areas of the Southeast where coyotes (*Canis latrans*) are severely reducing recruitment. The effect of male age structure on the timing and duration of the fawning season has yet to be firmly established, but I hypothesize managers can increase neonate development and survival by increasing male age structure.

Introduction

The intensity of management of white-tailed deer (*Odocoileus virginianus*) has increased prominently over the last two decades and has shifted from traditional management for maximum sustained yield to herds managed for quality. Quality deer management was designed to increase overall herd condition by harvesting an appropriate amount of antlerless deer relative

to available habitat and protecting young males from harvest (Miller and Marchinton 1995). Increases in antler size and hunter satisfaction are well documented byproducts of changes to population demography that occur under quality deer management, but how demography can affect the fawning season has received scant attention in the literature. It has been suggested that increased population age structure and a more balanced sex ratio, products of quality deer management, can alter the timing and duration of the breeding season (Guynn and Hamilton 1986, Jacobson 1992). In iteroparous mammalian species such as white-tailed deer, the timing of breeding season has evolved to allow fawns to be born during peak food availability, which helps ensure that females are able to meet the high nutritional demands of gestation and lactation (Verme 1965, Bronson 1989). The timing of the breeding season is adjustable as Jacobson (1992) found that breeding chronology shifted 2-3 weeks earlier with an increase in male age structure that was accomplished by protecting young males from harvest.

An earlier breeding season may be important for mitigating negative effects of late-born fawns. Research in the Southeast revealed late born fawns typically have smaller antlers (Gray et al. 2002) and bodies (Gray et al. 2002, Saalfeld et al. 2007) at age 1.5 than fawns born earlier in the season. Similarly, research on red deer (*Cervus elaphus*) revealed yearlings with small antlers were typically born later than yearlings with larger antlers (Schmidt et al. 2001). Conversely, fawns born earlier may have a fitness advantage over their late-born counterparts by having larger bodies and antlers at 1.5 years of age. Late-born fawns may be at a developmental disadvantage because food availability has passed its peak and nutritional availability relates directly to the amount of milk a female can provide (Verme 1965), in addition to having less time for development prior to winter. As for reproduction, female fawns born after the peak fawning period do not usually reach puberty their first breeding season (Verme and Ullrey 1984),

and male fawns may not develop spermatozoa in time to breed during their first rut (Peles et al. 2000). These studies suggest that birth date has impacts on development of fawns through their first few years.

Whereas timing of the fawning season is certainly important, the duration of the fawning season may be equally significant. Guynn and Hamilton (1986) found that breeding season condensed as adult sex ratio shifted from female biased to being balanced between the sexes. Synchrony of estrus among females during the breeding season may lead to greater survival of fawns the following summer (White et al. 2001). When fawns are born over a shorter time range, predators may be overwhelmed by the number of available prey, also known as predator swamping (Ims 1990, Whittaker and Lindzey 1999). Natural selection has guided fawning dates to occur during time periods conducive to successfully raising offspring, but the recent colonization of coyotes (*Canis latrans*) to southeastern ecosystems has introduced a different selective pressure to deer in this region. Several studies in the Southeast have recognized coyotes as being a key predator negatively impacting fawn recruitment (Saalfeld and Ditchkoff 2007, Howze et al. 2009, Kilgo et al. 2012, Jackson and Ditchkoff 2013, McCoy et al. 2013). Differences in the timing of the breeding season might explain why fawn recruitment is lower in areas of the Southeast, while other regions within the coyote's native range do not show similar impacts (Heugel et al. 1985, Brinkman et al. 2004, Grovenburn et al. 2011). The fawning season in the Southeast is typically later in the year compared to other areas of the white-tailed deer's range (Haugen 1959, Leuth 1967, Gray et al. 2002) which may exacerbate the negative influence coyotes are having on neonatal survival because coyote pups may be able to hunt by the time fawning occurs.

The effects of population demography on fawning season have yet to be clearly established, so my objective was to study effects of population age and sex ratio on the timing and duration of fawning season in central-Alabama during a fluctuating demography. Older (≥ 3.5 years old) males have been documented performing more ritualized breeding behavior than young (1.5 year old) males (Ozoga and Verme 1985), thus I predicted that as male structure became progressively mature, fawning dates would occur earlier (Guynn and Hamilton 1986, Jacobson 1992). I also predicted that fawning season duration would be more condensed when more mature males were present in the population (Guynn and Hamilton 1986, Miller et al. 1995).

Study Site

The deer in this study resided in the 174-hectare Auburn Captive Facility (ACF) located in Camp Hill, Alabama, USA. The population consisted of deer that were in the area at the time the fence was constructed in 2007, and their descendants. The perimeter of the ACF was bordered by a 2.6-meter deer-proof fence which allowed the study of individuals throughout their lifetime. Deer were fed 18% protein pellets (“Deer Feed,” SouthFresh Feeds, Demopolis, AL) ad libitum year round using 3 free choice feeders and their diet was supplemented by corn during fall and winter which helped attract deer for capture.

The two main cover types inside the ACF were open hayfields (40%) and mixed forest (60%). The predominant grass species found inside the ACF was bermuda grass (*Cynodon* sp.). Other grasses present included fescue (*Festuca* sp.), big bluestem (*Andropogon* sp.), Johnson grass (*Sorghum* sp.), dallisgrass (*Paspalum* sp.), and bahia grass (*Paspalum* sp.). The mixed forest species were oak (*Quercus* spp.), hickory (*Carya* spp.), maple (*Acer* spp.), and pine (*Pinus* spp.) of varying age. The general habitat within the wooded areas included a thick closed

canopy with little understory growth. Forest edges and creek bottoms contained dense understory growth consisting of Chinese privet (*Ligustrum sinense*). Water was available to deer from several creeks that ran throughout the property. Elevation ranged from 190 to 225 meters above sea level. The climate in this region of East-Central Alabama was moderately warm with mean high temperatures of 32.5 °C in July and mean low temperatures of -0.5°C in January. According to the National Oceanic and Atmospheric Administration weather station in Alexander City, Alabama (37 km northwest of our study area), average annual precipitation in the area was approximately 131 cm (National Climate Data Center 2013).

Methods

Vaginal Implant Transmitters (VITs, M3930, Advanced Telemetry Systems, Isanti, MN) were inserted from 2010 to 2013 in adult female deer beginning mid-February and ending in June using methods described by Saalfeld and Ditchkoff (2007). Females were captured using tranquilizer dart guns equipped with night vision scopes or a 0.8 ha modified box trap. Chemical immobilization occurred with an intramuscular injection of Telazol® (Fort Dodge Animal Health, Fort Dodge, Iowa; 125mg/ml given at a rate of 4.5 mg/kg) and xylazine (Lloyd Laboratories, Shenandoah, Iowa; 100mg/ml given at a rate of 2.2 mg/kg) followed by reversal with Tolazine® (Lloyd Laboratories, Shenandoah, Iowa; 100mg/ml given at a rate of 6.6 mg/kg; Miller et al. 2004). Deer were aged using the tooth replacement and wear (Severinghaus 1949). VITs were monitored once a week from insertion until 4 July, after which monitoring increased to 4 times per 24-hour period until the last transmitter had been expelled.

VITs were temperature sensitive so when expelled, the drop in temperature caused the pulse rate to double. Event time codes were programmed into the VITs so that expulsion time could be determined with an accuracy of ± 15 minutes. Upon detecting an expelled transmitter, I

used telemetry to home in on the VIT to help narrow the search area (Carstensen et al. 2003). A thermal imaging camera (Raytheon Palm IR 250D, Waltham, MA) was used to locate fawns not directly at the birth site. In these instances, the location of the VIT was used as a focal point of a grid search. Fawns were handled quickly (<10 minutes) to prevent any researcher induced abandonment (Powell et al. 2005), and data were collected from each fawn as part of another study (Acker 2013). Retention percentages were calculated by dividing the number of successful VITs (where a fawn was recovered) by the number of females implanted each year. All capture and handling procedures were in accordance with protocols approved by the Auburn University Institutional Animal Care and Use Committee (PRN numbers: 2008-1417, 2008-1421, 2010-1785, 2011-1971, and 2013-2372) and were in compliance with guidelines adopted by the American Society of Mammalogists Animal Care and Use Committee (Sikes et al. 2011).

Date of birth was recorded for each successful VIT expulsion and was converted to Julian date for statistical analysis. VITs that were expelled during the fawning season but not located at definitive birth sites were not included in analysis, as they were assumed to be premature expulsions, and birth could not be confirmed. I used ANOVA and *t*-tests in the program R to examine differences in fawning season between years (R Core Team 2012). I considered differences in fawning season significant at $\alpha \leq 0.05$. I also compared fawning season within the ACF to estimated fawning dates for adult female (≥ 2.5 years old) deer harvested within 40 km of our study site. These data were collected during spring reproductive surveys by the Alabama Department of Conservation and Natural Resources in Tallapoosa county using fetal measurements (Hamilton et al. 1985).

Results

Population reconstruction indicated minimum annual herd size ranged from 69 (2008) to 122 (2011) individuals (Table 2.1). Adult sex ratio gradually shifted over the course of the study from 1:2.0 M:F in 2008 to 1:0.8 M:F in 2012. Approximately 90% of adult deer were captured and marked as part of ongoing research at the study site. The proportion of known-age animals in the population increased from 50.7% in 2008 to 81.8% in 2013. Mean adult (>0.5 years old) male age increased from 1.42 in 2008 to 3.92 in 2013, while mean adult female age increased from 2.14 in 2008 to 4.17 in 2013.

From 2010 to 2013 a total of 55 females were fitted with VITs. I successfully recovered 37 neonates from 24 females. Successful VIT retention was 58.8, 30.0, 60.0, and 71.4% in 2010, 2011, 2012, and 2013, respectively. I censored 8 VITs from analysis in 2013 because batteries died before parturition occurred. A total of 6 VITs were retained nearly to parturition, but were not included in statistical analysis because I was unable to locate a birth site and thus confirm birth. Seventeen VITs were prematurely expelled before fawning season. Mean ages of implanted females were 3.7, 1.8, 3.2, and 5.7 years of age in 2010, 2011, 2012, and 2013, respectively. Females implanted in 2011 ($n = 3$) were 3.87 (± 3.66) years younger than females implanted in 2013 ($t = -3.21$, $P = 0.036$). Two females were implanted with VITs in multiple years, one of which was implanted for three consecutive years, with no adverse effects.

Mean fawning date occurred 12.4 (± 12.72 , 95% C.I.) days earlier in 2013 than in 2010 (Figure 2.1), however the difference was not significant ($t = 1.877$, $P = 0.109$). The length of fawning season ranged from 31 (Julian date 210 to 241, 29 July to 29 August) days in 2010 to 25 (208 to 233, 27 July to 21 August) days in 2011, but this difference was not significant ($t = 0.192$, $P = 0.895$). Mean fawning dates were 12 August ± 3.11 days ($\bar{x} \pm SE$), 10 August ± 7.45 days, 2 August ± 4.02 days, and 30 July ± 5.83 days for 2010, 2011, 2012, and 2013, respectively.

Mean fawning date did not differ from that of wild Alabama deer harvested in 2013 within 40 km of the ACF ($t = -0.441$, $P = 0.663$).

Discussion

I documented the trend toward an earlier fawning season as population demography changed. Although not significant, our low sample size and near significant results suggest that population demographics influenced the timing of parturition. Jacobson (1992) documented a similar shift toward earlier breeding when quality deer management harvest strategies increased male age structure. When there were more mature males present, the rut occurred 2-3 weeks earlier and was likely a result of more males available to breed females during their initial estrous cycle (Jacobson 1992). Our population mimicked the changes one would expect under quality deer management as male age structure increased over time. Older males have been documented to perform more ritualized breeding behavior than younger males (Ozoga and Verme 1985), which may explain the earlier fawning season I observed. The importance of population demography on breeding season has yet to be clearly established, but our results suggest that age structure of males can influence timing of the fawning season.

Although I was unable to test for significant differences in sex ratio over the course of our study, Guynn and Hamilton (1986) found that breeding season condensed as adult sex ratio shifted from female biased to being balanced between the sexes. I, however, did not document a significant shortening of the fawning season when more mature males were present in the population. Having more mature males relative to females in a population increases sexual competition and leaves fewer females unbred after their first estrous cycle (Miller et al. 1995), but sex ratios close to parity or slightly skewed toward females seem to function similarly. From 2010 to 2013, our population never had an estimated sex ratio less than 1 male for every 1.2

females, so I may not have been able to detect a condensed fawning season because sex ratios were already balanced when I began using VITs to document the fawning season. Similarly, Kilgo et al. (2012) found that fawning season at the Savannah River Site in South Carolina still occurred over a 2.5 month period, even when adult sex ratio approached parity for over 40 years. Although speculative, I believe the fawning season may have condensed since 2007 when the research facility was established, but I have no data on fawning season before VITs were utilized beginning in 2010.

Whether it is age structure or adult sex ratio affecting the fawning season, there is little doubt that late-born fawns are at a disadvantage relative to more earlier born from their cohort (Knox et al. 1991, Gray et al. 2002). In terms of physical development, late-born fawns typically have smaller antlers (Gray et al. 2002) and bodies (Gray et al, 2002, Saalfeld and Ditchkoff 2007) at age 1.5 than fawns born earlier in the season. Earlier breeding and fawning may have population level effects as earlier born female fawns may reach puberty and have offspring (Verme and Ullrey 1984). Conversely, late born female fawns usually do not breed, or if they do, it occurs late in the breeding season which perpetuates the late-born fawn cycle. Lifetime breeding success may also be influenced by birth date. Evidence suggests negative effects of late born fawns, such as small body size and reduced fecundity, may even persist into adulthood (Clutton-Brock et al. 1982, Mech et al. 1991, Monteith et al. 2009). Another disadvantage late born fawns incur is increased risk of winter mortality, especially in Northern regions where winter climates are severe (Delgiudice et al. 2006, Carstensen et al. 2009).

The timing of the fawning season is important as the relatively recent colonization of coyotes to southern regions is a concern to managers having to deal with reduced fawn survival. Although information is lacking for coyotes in the Southeast, they have been well studied within

their native range (Hilton 1978). Coyote pups are born in early spring and usually do not leave the vicinity of their den sites until 6-8 weeks old (Harrison and Gilbert 1985). These pups may be large enough to capture fawns by the time fawning season occurs in Alabama and some other parts of the Southeast (Saalfeld and Ditchkoff 2007). Having fawns born earlier in the growing season, may increase fawn survival because coyote pups may lack experience catching prey earlier in the year, or because pups have differential hunting tactics compared to older, more dominant coyotes (Gese et al. 1996). Selective pressures to have fawns born during a specific time period may become more pronounced as coyotes continue to persist on the Southeastern landscape. Despite the occurrence of coyotes at our study site, I failed to document any reduction in fawn recruitment. In areas where coyotes are negatively impacting fawn recruitment, harvest recommendations that influence deer population structure could mitigate some of these impacts (Kilgo et al. 2012).

Although having fawns born earlier and over a shorter time period can increase survival and development of fawns, there may be potential negative consequences found in populations that have increased proportions of mature males. The intense competition found in these populations can lead to elevated levels of injury and stress. In a population with a large proportion (>50%) of mature males (≥ 3.5 years old), Ditchkoff et al. (2001) reported mortality of mature males due to rut-related stress and physical exertion was greater than human-induced hunting mortality, and speculated that this was due to the high proportion of mature males in the population and associated levels of competition for breeding. Ozoga and Verme (1985) observed evidence of differential participation in breeding activity between old (≥ 3.5 year olds) and young (1.5 year olds) males by manipulating male age structure within a population. When only 1.5 year old males were present, they observed fewer rubs and scrapes than when only older males

were present, but no differences in adult male survival were reported. Another potential consequence of managing populations for increased numbers of older males is increased risk of intracranial abscessation, which is thought to be caused by breeding activities such as antler sparring, rubbing, or antler casting (Davidson et al. 1990). It has been reported that intracranial abscessation can be a significant cause of mortality in older males (Davidson et al. 1990, Karns et al. 2009). Antler breakage patterns are also of management importance as they may be indicative of a population with a high proportion of mature males (Karns and Ditchkoff 2012). Although I did not collect data on antler breakage, anecdotal evidence suggests more breakage occurred in 2013 than in 2008, which also suggests that competition for females in the ACF was more intense in 2013 compared to 2008.

Although male demographics are certainly important, female nutrition and age also play an important role as to when an individual will enter estrus (Abler et al. 1976) and give birth (Verme 1969). Gestation may be extended for females in poor condition while females in good condition may not gestate as long (Verme 1965). The nutritional plane (due to supplemental feed provided ad libitum) and age of females fitted with VITs was consistent throughout the study to isolate the effect of population demographics on fawning date. I did not collect data on native forage availability during our study, and low sample size prevented any comparisons of female age to fawning date. Guynn and Hamilton (1986) found that female age was not an important determinant of when breeding occurred. They documented an earlier shift in the breeding season even as the age of pregnant females at their study site slightly declined. If age were an important factor, they should have found later conception dates when younger females were present.

I documented an earlier fawning season with increasing male age structure, which supports the notion that having more mature males present in a population has a positive influence on fawning date. Earlier-born fawns get a head start on development which may persist into adulthood. Managers seeking to improve fawn survival as well as allow more time to develop prior to winter may consider increasing male age structure, which increases breeding competition and results in earlier fawning. The positive effects of earlier fawning may not be apparent the first season quality deer management is implemented, but benefits should continue to accrue into successive years of the management program as early born fawns reach maturity. In addition to the positive impacts on fawn development, an earlier fawning season may also be good for managers seeking to counteract reduced fawn survival caused by coyote predation.

Acknowledgments

This study was supported by the Alabama Agriculture Experiment Station, Center for Forest Sustainability, and School of Forestry and Wildlife Sciences, Auburn University. I appreciate the assistance of many volunteer technicians that helped monitor transmitters and aided in data collection.

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Table 2.1 – Known white-tailed deer breeding populations by sex, age class, and cohort birth year from 2008-2013, Auburn Captive Facility, Camp Hill AL.

Age	2008	2009	2010	2011	2012	2013
Total popln. ^a	69 (35 ^b)	84 (51 ^b)	98 (63 ^b)	122 (90 ^b)	114 (89 ^b)	110 (90 ^b)
Males	25 (15)	40 (29)	48 (34)	62 (50)	64 (53)	53 (45)
0.5	11 (9)	16 (15)	14 (11)	21 (21)	13 (13)	8 (8)
1.5	8 (6)	10 (8)	13 (12)	11 (8)	12 (12)	9 (9)
2.5	3 (0)	8 (6)	9 (7)	12 (11)	11 (8)	6 (6)
3.5	3 (0)	3 (0)	6 (4)	8 (6)	11 (10)	9 (6)
4.5	0	3 (0)	3 (0)	6 (4)	8 (6)	8 (8)
5.5	0	0	3 (0)	2 (0)	6 (4)	7 (5)
6.5	0	0	0	2 (0)	2 (0)	4 (3)
7.5	0	0	0	0	1 (0)	1 (0)
8.5	0	0	0	0	0	1 (0)
Females	44 (20)	44 (22)	50 (29)	60 (40)	50 (36)	48 (36)
0.5	16 (11)	7 (6)	13 (10)	12 (12)	9 (9)	6 (6)
1.5	7 (6)	14 (9)	5 (4)	13 (10)	10 (10)	9 (9)
2.5	8 (3)	5 (4)	13 (8)	5 (4)	8 (5)	8 (8)
3.5	7 (0)	7 (3)	5 (4)	12 (7)	3 (3)	5 (2)

Table 2.1 – Continued

Age	2008	2009	2010	2011	2012	2013
4.5	4 (0)	5 (0)	6 (3)	5 (4)	9 (4)	3 (3)
5.5	1 (0)	4 (0)	4 (0)	6 (3)	4 (3)	8 (4)
6.5	0	1 (0)	2 (0)	3 (0)	5 (2)	4 (3)
7.5	1 (0)	0	1 (0)	2 (0)	1 (0)	3 (1)
8.5	0	1 (0)	0	1 (0)	1 (0)	1 (0)
9.5	0	0	1 (0)	0	0	1 (0)
10.5	0	0	0	1 (0)	0	0
Sex Ratio						
(M:F) ^c	1:2.0	1:1.5	1:1.1	1:1.2	1:0.8	1:0.9

^a Abundances estimated using combination of camera surveys, field observations, capture of live animals, and recovery of deceased animals. All estimating methods indicated $\geq 90\%$ of animals in population were marked during the study yielding largely known population sizes.

^b Number of individuals initially captured at ≤ 2.5 years old.

^c For animals >0.5 years old.

Figure 2.1 – Julian birth dates of white-tailed deer fawns captured from 2010 - 2013 using vaginal implant transmitters at the Auburn Captive Facility, Camp Hill, AL.

