



Microsatellites reveal plasticity in reproductive success of white-tailed deer

TIMOTHY J. NEUMAN, CHAD H. NEWBOLT, STEPHEN S. DITCHKOFF,* AND TODD D. STEURY

School of Forestry and Wildlife Sciences, 602 Duncan Drive, Auburn University, Auburn, AL 36849, USA (TJN, CHN, SSD, TDS)

* Correspondent: ditchss@auburn.edu

Mate choice based on age and body size is poorly understood among cervids. We used 14 microsatellite DNA loci to assign parentage and reconstruct the pedigree of a captive population of white-tailed deer (*Odocoileus virginianus*) in order to evaluate their mate choice and reproductive success. From 2008 to 2013, we assigned both dam and sire to 87 litters. Age differences between mated pairs did not differ from random pairings and we found no apparent relationship of skeletal size between pairs. Our results highlight the plasticity of mating success for white-tailed deer and we speculate their mating system has evolved to maximize fertility. Our investigation was the first to explore mated pairs of white-tailed deer 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 of white-tailed deer.

Key words: CERVUS, mate choice, microsatellites, reproductive success, vaginal implant transmitters, white-tailed deer

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 theories for the cause of sexual dimorphism are 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 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 h (Hirth 1977).

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 attributes of males such as age (Sorin 2004; DeYoung et al. 2009) and body size (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; DelGiudice et al. 2007). The results of each study differ by region and nutritional availability, but the trend is similar between areas; fawns rarely breed, yearlings usually have 1 fawn, and 2.5+ year olds produce more twins than younger age classes.

While individual male and female physical attributes are certainly important when trying to understand breeding success of white-tailed deer, 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 years 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.

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 intramale 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, we monitored a captive population of white-tailed deer exhibiting natural breeding behavior and evaluated mate choice using offspring parentage assignments. Our 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. Another goal was to observe how age and body size influence number of offspring produced. We predicted age and body size would be positively correlated between mated pairs as individuals concurrently seek to maximize fitness ([Berger 1989](#); [Sorin 2004](#)). We predicted that older, larger females would mate with large, similar-aged males and produce more offspring than younger, smaller females ([Ozoga and Verme 1986b](#); [Nixon and Etter 1995](#)). We predicted that younger males that successfully bred were larger than similar-aged males 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-ha Auburn Captive Facility (ACF) located in

Camp Hill, Alabama. The population consisted of deer that were in the area at the time of constructing in 2007 and their descendants. The perimeter of the ACF was bordered by a 2.6-m 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, Alabama) ad libitum year round using 3 free choice feeders. Their diet was supplemented by 4 timed feeders providing approximately 2 kg/day of corn during fall and winter which helped attract deer for capture.

The 2 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 m 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. While predators (*Canis latrans* and *Lynx rufus*) were present in the enclosure throughout the study, fawn recruitment estimated by monitoring survival of radiocollared fawns was $> 50\%$ (T. J. Neuman, pers. obs.).

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; 125 mg/ml given at a rate of 4.5 mg/kg) and xylazine (Lloyd Laboratories, Shenandoah, Iowa; 100 mg/ml given at a rate of 2.2 mg/kg) followed by reversal with an intramuscular injection of Tolazine (Lloyd Laboratories, Shenandoah, Iowa; 100 mg/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 1 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, Pennsylvania) 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. 1997). Deer were aged using tooth replacement and wear (Severinghaus 1949). Although this method has come under recent scrutiny (Gee et al. 2002), we minimized potential errors by limiting aging assignments to 3 biologists 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 premolars. Deer initially captured and aged ≤ 1.5 years were considered known-age for the remainder of the 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 (hereafter VITs, M3930, Advanced Telemetry Systems, Isanti, Minnesota) following procedures described by Saalfeld and Ditchkoff (2007). VITs were placed in females captured from late February to early June. We monitored VITs every 6 hours during the fawning season to determine if the transmitter was expelled. A thermal imaging camera (Raytheon Palm IR 250D, Waltham, Massachusetts) was used to locate 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 us to view all animals at one time; therefore, we used a combination of methods to estimate population demographics. We used infrared-triggered camera surveys conducted biannually at sites baited with shelled corn and along trails (Jacobson et al. 1997; Karanth and Nichols 1998; McCoy et al. 2011). Ear tags, freeze brands, and unique antler configurations allowed us to identify individuals and estimate abundance, sex ratio, proportion of adults sampled, and age structure of the population. Marked individuals were not fitted with mortality detectors which created some uncertainty regarding prolonged absence of some individuals from the camera surveys. We 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. We used camera survey data in conjunction with

current capture and mortality records to reconstruct the total population during the breeding season 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. We captured 10 individuals (5 females, 5 males) < 1 year 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.—Fourteen microsatellite markers were scored by DNA Solutions (Oklahoma City, Oklahoma) using the panel first described by Anderson et al. (2002). DNA Solutions was ISO17025 accredited and all samples were run with positive and negative controls. We 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).

We defined reproductive success as the successful birth of offspring or the siring of a fawn by males. Our sample did not include fetuses or fawns that were born and died prior to us being able to capture them and collect a tissue sample, and thus our data do not account for all breedings, nor provide a complete accounting of reproductive success. The 6 years of reproductive success data were divided into yearly offspring cohorts, meaning we 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, we simulated 10,000 replications of offspring parentage using known population demographics which included number of candidate parents, percentage of sampled individuals, and typing error rates. Simulations provided critical values for the Delta statistic which CERVUS used when assigning parentage. Our typing error rate was 0.014 which was calculated in CERVUS using known mother–offspring pairings obtained with the aid of VITs. Accuracy of CERVUS parentage assignments was calculated by including all living females as candidate mothers and comparing results to known mother–offspring pairings obtained with the aid of VITs, which were not included in our analyses of mated pairs. 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 likelihood of difference 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.—We used data from 6 years (2008–2013) of reproductive success inside the ACF to determine physical attributes between mated pairs. For female reproductive success, we 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 reflected this difference (Ditchkoff et al. 1997; Ditchkoff 2011). Male skeletal body sizes were grouped into 6 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 3 categories: fawns, 1.5, and 2.5+ years old. Body size relationships between mated pairs were analyzed using linear regression in R (R Core Development Team, version 15.3, accessed 15 December 2013). Age relationships were examined using a chi-square test, comparing observed age

differences between mated pairs to expected age differences of available mated pairs assuming random mating.

We were 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, we used percentiles. We calculated percentiles by pooling all measurements across all years and grouped them by age. We 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), we 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, we calculated the mean percentile score of his lifetime body size and used that number in our correlation of body size if he sired offspring at 4.5 years old.

RESULTS

Demography.—Population estimating methods indicated that minimum annual herd size ranged from 69 to 122 individuals from 2008 to 2013 (Table 1). Initial adult sex ratio was 1:2 M:F, which gradually shifted toward parity with an estimated ratio of 1:0.9 M:F in 2013. Approximately 90% of adult deer had been captured and marked. The proportion of known-age

Table 1.—Known white-tailed deer breeding populations by sex, age class, and cohort birth year from 2008 to 2013, Auburn Captive Facility, Camp Hill, Alabama.

Age	2008	2009	2010	2011	2012	2013
Total population ^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)
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.

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 2.14 (± 0.225 SE, $n = 14$) in 2008 to 3.92 (± 0.272 , $n = 45$) in 2013, while mean adult female age increased from 3.07 (± 0.269 , $n = 28$) in 2008 to 4.17 (± 0.345 , $n = 42$) in 2013. Initial density was 0.4 deer/ha in 2007 and peaked in 2011 at 0.7 deer/ha.

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 2). Allelic richness ranged from 4 to 16 alleles per locus ($\bar{X} = 9.93$). Equilibrium tests revealed linkage disequilibrium

Table 2.—Population genetics information (individual locus allelic richness, gene diversity, F_{IS} , and Hardy–Weinberg probabilities) for white-tailed deer from 2008 to 2013 at Auburn Captive Facility, Camp Hill, Alabama.

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.

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. 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 10 individuals born in 2012 remained uncaptured when data were analyzed.

Parentage.—We assigned both sire and dam to 87 litters at the 95% confidence level. Twenty-four of 87 (27.6%) assigned dams were known-age (dam was originally captured at 0.5 or 1.5 years of age), whereas 30 of 87 (34.5%) assigned sires were known-age (sire was originally captured at 0.5 or 1.5 years of 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). 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. 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 1 case of same-aged males occurred between dissimilar sized males.

Herd reconstruction using assigned parentage allowed us to compute minimum recruitment values for females. Reproductive success for females ≥ 2.5 years old did not vary

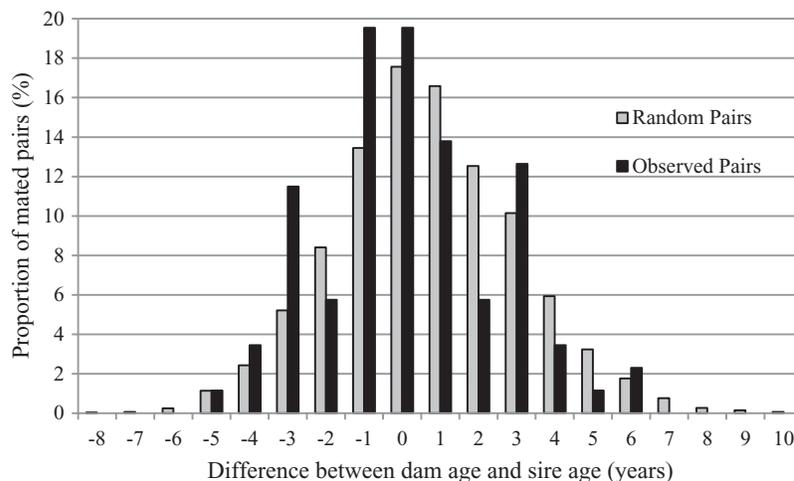


Fig. 1.—Observed age differences between white-tailed deer (*Odocoileus virginianus*) dams and sires from 2008 to 2013, and age differences assuming the occurrence of random mating, Auburn Captive Facility, Camp Hill, Alabama.

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 $0.76 (\pm 0.077, n = 13)$. We documented 9 female fawns that recruited offspring into the fall population, and they each recruited 1 individual. Females ≤ 1.5 years old failed to recruit more than 1 offspring during the study period. Two different females each recruited 1 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.

The smallest young-of-the-year females produced essentially 0 fawns. For each 1-year increase in age, those females produced 130 (5.36–3229; 95% confidence limit) times as many fawns ($z = 2.56, df = 79, P = 0.002$) as they produced a year earlier. Similarly, for each 10-cm increase in skeletal size, the youngest females produced 2 (1.29–3.12) times as many fawns ($z = 3.34, df = 79, P = 0.0006$). However, there was a significant interaction between age and size ($z = 2.48, df = 79, P = 0.003$) such that as females got older, the effects of size

decreased. Similarly, as females became larger, the effects of age decreased. Additionally, we found no relationship ($t = 1.48, df = 16, P = 0.158$) between skeletal sizes of 18 mated pairs for which we had measurements of both parents (Fig. 3). Using lifetime body percentile as a surrogate for body size allowed us to compare size relationships for 82 mated pairs, which also resulted in no relationship ($t = 0.487, df = 81, P = 0.628$; Fig. 4).

DISCUSSION

Our findings do not support our original hypothesis that female 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 our results indicate 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. Our

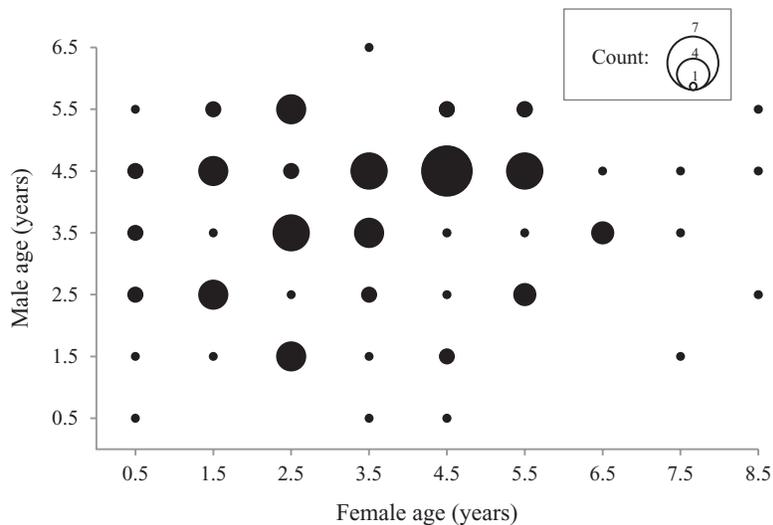


Fig. 2.—Range-graded dot representation of age relationships between mated pairs of white-tailed deer (*Odocoileus virginianus*) from 2008 to 2013, Auburn Captive Facility, Camp Hill, Alabama.

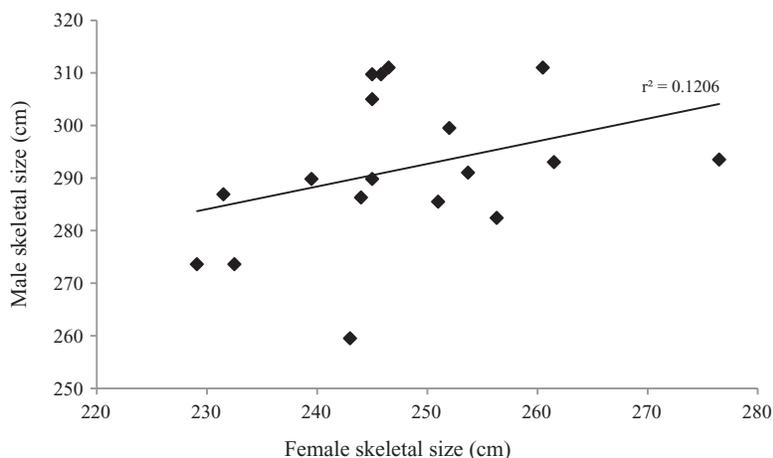


Fig. 3.—Size comparison of 18 mated pairs of white-tailed deer (*Odocoileus virginianus*) for which measurements were available for both parents from 2008 to 2013, Auburn Captive Facility, Camp Hill, Alabama.

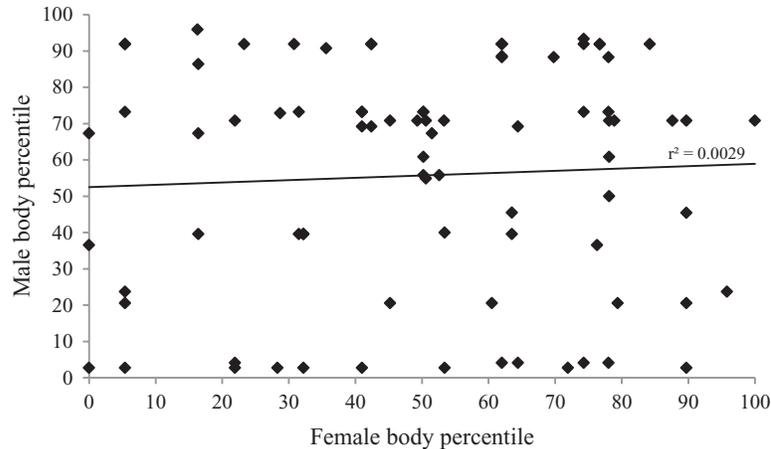


Fig. 4.—Body percentile comparison between mated pairs of white-tailed deer (*Odocoileus virginianus*) from 2008 to 2013, Auburn Captive Facility, Camp Hill, Alabama.

results show that older females will tolerate advances made by young males, with evidence of an extreme example in 2008 when a 1.5-year-old male mated with a 7.5-year-old female. [Schultz and Johnson \(1992\)](#) documented male fawns breeding which we also observed when older males were present. [Ozoga and Verme \(1985\)](#) indicated 1.5-year-old males gained mating opportunities with females of all ages, although no older males were present during their observations. [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 use physical characteristics such as body size and behavioral characteristics such as dominance ([Townsend and Bailey 1981](#)). 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. We noticed female skeletal size was associated with a female's ability to have more offspring. We 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 pursue females based on chemical signals regarding receptiveness ([Murphy et al. 1994](#)) rather than physical attributes.

The wide range of ages and body sizes we 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 1st 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 that 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. On the day the females entered estrus, however, their demeanor changed and they stood quietly and calmly until serviced ([Haugen 1959](#)). Although speculative, we 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](#); [DelGiudice et al. 2007](#)), which may explain why seemingly poor quality mates of both sexes successfully breed.

The mate choice decision is confounded by the role population demographics plays 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](#)). We observed that as the male age structure matured, the proportion of breeding by 1.5-year-old males decreased. 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, 1 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 1st 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.

We 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 nonpregnant does. 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). We 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. 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. We noticed a significant interaction between age and body size such that with increasing age, the smallest females were still successful breeders, and size was a strong determinant of success among the youngest females. 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 fewer fawns than older, larger deer: but only to a certain age. However, it is likely that the availability of supplemental feed raised the nutritional plane of the herd and may have masked some differences in reproductive success among females of varying condition.

Although our observations of mated pairs were derived with small sample sizes from only 1 population, similar tendencies would be expected across the white-tailed deer's range. We 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. Multiyear 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, we were able to collect detailed data from most individuals in the population, enabling us 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, 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), we feel our data are representative of behaviors and mate choices found in a free-range setting.

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 navigate the landscape to 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. 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.

We thank V. Jackson for maintaining feeders and habitat within our study site. We appreciate the assistance of R. DeYoung when analyzing our genetic data. Many undergraduate volunteer technicians from the School of Forestry and Wildlife Sciences at Auburn University helped monitor transmitters and assist in data collection, most notably C. Glassey, J. Garrett, and J. Brooks. Additional thanks to M. Smith for reviewing our manuscript.

LITERATURE CITED

- ANDERSON, J. D., ET AL. 2002. Development of microsatellite DNA markers for the automated genetic characterization of white-tailed deer populations. *Journal of Wildlife Management* 66:67–74.
- ANDERSSON, M. 1994. *Sexual selection*. Princeton University Press, Princeton, New Jersey.
- BATEMAN, A. J. 1948. Intra-sexual selection in *Drosophila*. *Heredity* 2:349–368.
- BERGER, J. 1989. Female reproductive potential and its apparent evaluation by male mammals. *Journal of Mammalogy* 70:347–358.
- CLUTTON-BROCK, T. H., S. D. ALBON, AND F. E. GUINNESS. 1989. Fitness costs of gestation and lactation in wild mammals. *Nature* 337:260–262.
- CLUTTON-BROCK, T. H., F. E. GUINNESS, AND S. D. ALBON. 1982. *Red deer: behavior and ecology of two sexes*. University of Chicago Press, Chicago, Illinois.
- DELGIUDICE, G. D., M. S. LENARZ, AND M. CARSTENSEN POWELL. 2007. Age-specific fertility and fecundity in northern free-ranging white-tailed deer: evidence for reproductive senescence? *Journal of Mammalogy* 88:427–435.
- DEYOUNG, R. W., S. DEMARAIS, K. L. GEE, R. L. HONEYCUTT, M. W. HELICKSON, AND R. A. GONZALES. 2009. Molecular evaluation of the white-tailed deer (*Odocoileus virginianus*) mating system. *Journal of Mammalogy* 90:946–953.
- DEYOUNG, R. W., S. DEMARAIS, R. A. GONZALES, R. L. HONEYCUTT, AND K. L. GEE. 2002. Multiple paternity in white-tailed deer (*Odocoileus virginianus*) revealed by DNA microsatellites. *Journal of Mammalogy* 83:884–892.
- DITCHKOFF, S. S. 2011. Anatomy and physiology. Pp. 43–73 in *Biology and management of white-tailed deer* (D. G. Hewitt, ed.). CRC Press, Boca Raton, Florida.
- DITCHKOFF, S. S., E. R. WELCH, JR., W. R. STARRY, W. C. DINKINES, R. E. MASTERS, AND R. L. LOCHMILLER. 1997. Quailty deer management at the McAlester army ammunition plant: a unique approach. *Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies* 51:389–399.
- EL MOUSADIK, A., AND R. J. PETIT. 1996. High level of genetic differentiation for allelic richness among populations of the argan tree [*Argania spinosa* (L.) Skeels] endemic to Morocco. *Theoretical and Applied Genetics* 92:832–839.
- EMLEN, S. T., AND L. W. ORING. 1977. Ecology, sexual selection, and evolution of mating systems. *Science* 197:215–223.
- FOLK, M. J., AND W. D. KLIMSTRA. 1991. Reproductive-performance of female key deer. *Journal of Wildlife Management* 55:386–390.
- GEE, K. L., J. H. HOLMAN, M. K. CAUSEY, A. N. ROSSI, AND J. B. ARMSTRONG. 2002. Aging white-tailed deer by tooth replacement and wear: a critical evaluation of a time-honored technique. *Wildlife Society Bulletin* 30:387–393.
- GOUDET, J. 1995. FSTAT: a computer program to calculate F-statistics. Version 1.2. *Journal of Heredity* 86:485–486.
- GOUDET, J. 2001. FSTAT, a program to estimate and test gene diversities and fixation indices. Version 2.9.3. <http://www2.unil.ch/pop-gen/softwares/fstat.htm> [updated from Goudet 1995]. Accessed 4 December 2013.
- GRAY, W. N., II, S. S. DITCHKOFF, K. CAUSEY, AND C. W. COOK. 2002. The yearling disadvantage in Alabama deer: effect of birth date on development. *Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies* 56:255–264.
- HAUGEN, A. O. 1959. Breeding records of captive white-tailed deer in Alabama. *Journal of Mammalogy* 40:108–113.
- HAUGEN, A. O. 1975. Reproductive-performance of white-tailed deer in Iowa. *Journal of Mammalogy* 56:151–159.
- HIRTH, 1977. Social behavior of white-tailed deer in relation to habitat. *Wildlife Monographs* 53:1–55.
- ISAAC, J. L. 2005. Potential causes and life-history consequences of sexual size dimorphism in mammals. *Mammal Review* 35:101–115.
- JACOBSON, H. A., J. C. KROLL, R. W. BROWNING, B. H. KOERTH, AND M. H. CONWAY. 1997. Infrared-triggered cameras for censusing white-tailed deer. *Wildlife Society Bulletin* 25:547–556.
- JONES, P. D., B. K. STRICKLAND, S. DEMARAIS, AND R. W. DEYOUNG. 2011. Inconsistent association of male body mass with breeding success in captive white-tailed deer. *Journal of Mammalogy* 92:527–533.
- KALINOWSKI, S. T., M. L. TAPER, AND T. C. MARSHALL. 2007. Revising how the computer program CERVUS accommodates genotyping error increases success in paternity assignment. *Molecular Ecology* 16:1099–1106.
- KARANTH, K. U., AND J. D. NICHOLS. 1998. Estimation of tiger densities in India using photographic captures and recaptures. *Ecology* 79:2852–2862.
- KIE, J. G., AND M. WHITE. 1985. Population-dynamics of white-tailed deer (*Odocoileus virginianus*) on the welder wildlife refuge, Texas. *Southwestern Naturalist* 30:105–118.
- KILPATRICK, H. J., A. J. DENICOLA, AND M. R. ELLINGWOOD. 1996. Comparison of standard and transmitter-equipped darts for capturing white-tailed deer. *Wildlife Society Bulletin* 24:306–310.
- LONG, E. S., D. R. DIEFENBACH, C. S. ROSENBERRY, B. D. WALLINGFORD, AND M. R. D. GRUND. 2005. Forest cover influences dispersal distance of white-tailed deer. *Journal of Mammalogy* 86:623–629.
- MARGULIS, S. W. 1993. Mate choice in rocky-mountain mule deer bucks (*Odocoileus hemionus hemionus*) is there a preference for does without fawns? *Ethology Ecology & Evolution* 5:115–119.
- MARTIN, J. G. A., AND M. FESTA-BIANCHET. 2010. Bighorn ewes transfer the costs of reproduction to their lambs. *American Naturalist* 176:414–423.
- MCCOY, J. C., S. S. DITCHKOFF, AND T. D. STEURY. 2011. Bias associated with baited camera sites for assessing population characteristics of deer. *Journal of Wildlife Management* 75:472–477.
- MECH, L. D., AND R. E. McROBERTS. 1990. Survival of white-tailed deer fawns in relation to maternal age. *Journal of Mammalogy* 71:465–467.
- MILLER, B. F., L. I. MULLER, T. DOHERTY, D. A. OSBORN, K. V. MILLER, AND R. J. WARREN. 2004. Effectiveness of antagonists for tiletamine-zolazepam/xylazine immobilization in female white-tailed deer. *Journal of Wildlife Diseases* 40:533–537.
- MUNDINGER, J. G. 1981. White-tailed deer reproductive-biology in the swan valley, Montana. *Journal of Wildlife Management* 45:132–139.
- MURPHY, B. P., K. V. MILLER, AND R. L. MARCHINTON. 1994. Sources of reproductive chemosignals in female white-tailed deer. *Journal of Mammalogy* 75:781–786.

- NATIONAL RESEARCH COUNCIL. 2007. Nutrient requirements of small ruminants: sheep, goats, cervids, and new world camelids. National Academies Press, Washington, D.C.
- NEI, M. 1973. Analysis of gene diversity in subdivided populations. *Proceedings of the National Academy of Sciences of the United States of America* 70:3321–3323.
- NIXON, C. M., AND D. ETTER. 1995. Maternal age and fawn rearing success for white-tailed deer in Illinois. *American Midland Naturalist* 133:290–297.
- OZOGA, J. J. 1987. Maximum fecundity in supplementally-fed northern michigan white-tailed deer. *Journal of Mammalogy* 68:878–879.
- OZOGA, J. J., AND L. J. VERME. 1982. Physical and reproductive characteristics of a supplementally-fed white-tailed deer herd. *Journal of Wildlife Management* 46:281–301.
- OZOGA, J. J., AND L. J. VERME. 1985. Comparative breeding-behavior and performance of yearling vs prime-age white-tailed bucks. *Journal of Wildlife Management* 49:364–372.
- OZOGA, J. J., AND L. J. VERME. 1986a. Initial and subsequent maternal success of white-tailed deer. *Journal of Wildlife Management* 50:122–124.
- OZOGA, J. J., AND L. J. VERME. 1986b. Relation of maternal age to fawn-rearing success in white-tailed deer. *Journal of Wildlife Management* 50:480–486.
- PEKINS, P. J., K. S. SMITH, AND W. W. MAUTZ. 1998. The energy cost of gestation in white-tailed deer. *Canadian Journal of Zoology* 76:1091–1097.
- PELES, J. D., O. E. RHODES, AND M. H. SMITH. 2000. Spermatozoan numbers and testicular characteristics of male white-tailed deer fawns during the mating season. *Acta Theriologica* 45:95–102.
- RHODES, O. E., JR., K. T. SCRIBNER, M. H. SMITH, AND P. E. JOHNS. 1985. Factors affecting the number of fetuses in a white-tailed deer herd. *Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies* 39:380–388.
- RICE, W. R. 1989. Analyzing tables of statistical tests. *Evolution* 43:223–225.
- SAALFELD, S. T., AND S. S. DITCHKOFF. 2007. Survival of neonatal white-tailed deer in an exurban population. *Journal of Wildlife Management* 71:940–944.
- SCHULTZ, S. R., AND M. K. JOHNSON. 1992. Breeding by male white-tailed deer fawns. *Journal of Mammalogy* 73:148–150.
- SEVERINGHAUS, C. W. 1949. Tooth development and wear as criteria of age in white-tailed deer. *Journal of Wildlife Management* 13:195–216.
- SIKES, R. S., W. L. GANNON, AND THE ANIMAL CARE AND USE COMMITTEE OF THE AMERICAN SOCIETY OF MAMMALOGISTS. 2011. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. *Journal of Mammalogy* 92:235–253.
- SORIN, A. B. 2004. Paternity assignment for white-tailed deer (*Odocoileus virginianus*): mating across age classes and multiple paternity. *Journal of Mammalogy* 85:356–362.
- THERRIEN, J. F., S. D. COTE, M. FESTA-BIANCHET, AND J. P. OUELLET. 2007. Conservative maternal care in an iteroparous mammal: a resource allocation experiment. *Behavioral Ecology and Sociobiology* 62:193–199.
- TOWNSEND, T. W., AND E. D. BAILEY. 1981. Effects of age, sex and weight on social rank in penned white-tailed deer. *American Midland Naturalist* 106:92–101.
- TRIVERS, R. L. 1972. Parental investment and sexual selection. Pp. 136–207 in *Sexual selection and the descent of man 1871–1971* (B. G. Campbell, ed.). Aldine Publishing Company, Chicago, Illinois.
- VERME, L. J. 1969. Reproductive patterns of white-tailed deer related to nutritional plane. *Journal of Wildlife Management* 33:881–889.
- VERME, L. J., AND D. E. ULLREY. 1984. Physiology and nutrition. Pp. 91–118 in *White-tailed deer: ecology and management* (L. K. Halls, ed.). Stackpole Books, Harrisburg, Pennsylvania.
- WEIR, B. S., AND C. C. COCKERHAM. 1984. Estimating f-statistics for the analysis of population-structure. *Evolution* 38:1358–1370.
- WHITTAKER, D. G., AND F. G. LINDZEY. 1999. Effect of coyote predation on early fawn survival in sympatric deer species. *Wildlife Society Bulletin* 27:256–262.
- ZWANK, P. J., AND J. A. ZENO. 1986. Weight of white-tailed deer fawns relative to fawning date. *Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies* 40:424–429.

Submitted 26 January 2016. Accepted 14 April 2016.

Associate Editor was Marjorie D. Matocq.