

## Featured Article

# Factors Influencing Reproductive Success in Male White-Tailed Deer

CHAD H. NEWBOLT,<sup>1</sup> *School of Forestry and Wildlife Sciences, Auburn University, AL 36849, USA*

PETER K. ACKER, *School of Forestry and Wildlife Sciences, Auburn University, AL 36849, USA*

TIMOTHY J. NEUMAN, *School of Forestry and Wildlife Sciences, Auburn University, AL 36849, USA*

STEPHANIE I. HOFFMAN, *School of Forestry and Wildlife Sciences, Auburn University, AL 36849, USA*

STEPHEN S. DITCHKOFF, *School of Forestry and Wildlife Sciences, Auburn University, AL 36849, USA*

TODD D. STEURY, *School of Forestry and Wildlife Sciences, Auburn University, AL 36849, USA*

**ABSTRACT** Positive relationships between age, sexually selected traits, and male reproductive success have been reported for a number of polygynous ungulates; however, relatively little is known about the factors influencing male reproductive success in ungulate species whose mating system is characterized by tending-bond behaviors. Broad interest in the genetic consequences of selective harvest supports a greater understanding of the role of these factors as determinants of male reproductive success in important game species (e.g., white-tailed deer [*Odocoileus virginianus*]), that exhibit tending-bond behaviors. We investigated male reproductive success in white-tailed deer across a range of sex ratios and age structures using a known population of deer housed in a 175-ha enclosure in central Alabama, USA. We measured age, annual antler size, and annual body size of male white-tailed deer and assigned paternity to 143 known-age offspring during 2007–2014. Reproductive success was attributed to a high proportion of males during each of the 6 breeding seasons. Our most supported model indicated that annual body size and antler size of the individual were positively associated with annual male breeding success. The effects of annual antler size were sensitive to changes in mean male age of the herd, with antler size having the greatest effect on male reproductive success under older male age structures. Young ( $\leq 1.5$  yr) males reproduced most frequently when male age structure was youngest (which correlated with female-biased sex ratios in this population). Our results suggest that male age structure and sex ratio played a key role in establishing patterns of male reproductive success in white-tailed deer. Management practices that encourage balanced adult sex ratios and older male age structures (e.g., Quality Deer Management) may promote a highly competitive environment where sexually selected traits are of increased importance to male breeding success. However, the ability of managers to alter herd genetics in a positive or negative direction through selective harvest is limited in white-tailed deer because of the high proportion of reproducing males. © 2016 The Wildlife Society.

**KEY WORDS** breeding behavior, life history, reproductive success, sexual selection, ungulate, white-tailed deer.

Selection theory suggests that sexual size dimorphism and secondary sexual characteristics (e.g., antlers, horns, tusks) are evolved and perpetuated in some mammals as a result of reproductive advantages (Geist 1966, Andersson 1994). Competition among males for access to mates is fundamental to sexual selection, and, consequently, variables that shape the competitive environment (e.g., duration of breeding season, population density) are important influences of sexually selected traits (Andersson 1994, Gosden and Svensson 2008, Martin et al. 2016). Polygynous ungulate mating systems frequently are characterized by short breeding seasons and intense competition among males for mates, and the selective

pressures that arise under these conditions are thought to have contributed to the high level of sexual dimorphism and large horns and antlers found in many of these species (Clutton-Brock et al. 1979, Hendrick and Temeles 1989, Coltman et al. 2002, Mysterud et al. 2003, Ciuti and Apollonio 2016). Positive relationships between male reproductive success, body size, and horn and antler size have been reported for numerous ungulate species, including red deer (*Cervus elaphus*), fallow deer (*Dama dama*), and bighorn sheep (*Ovis canadensis*; Clutton-Brock et al. 1988; McElligott et al. 2001; Coltman et al. 2002; Kruuk et al. 2002, 2014). Physical traits are correlated with age in many ungulate species, and, as such, male reproductive success generally is higher for prime-aged males than young or senescent individuals (Festa-Bianchet 2012).

The relative importance of age, body size, and antler and horn size as determinants of male reproductive success varies

Received: 22 January 2016; Accepted: 10 October 2016

<sup>1</sup>E-mail: newboch@auburn.edu

between ungulate species (Clutton-Brock et al. 1988, Hogg and Forbes 1997, Coltman et al. 1999, McElligott et al. 2001, Willisch et al. 2012). Male polygynous ungulates exhibit a variety of mate guarding behaviors, including resource defense, harem defense, lekking, and tending, and the adopted behaviors influence the role of male traits in reproduction (Hogg 1987, Clutton-Brock et al. 1988, Clutton-Brock 1989, Marino 2012, Ciuti and Apollonio 2016). For example, reproductive success in populations of red deer that exhibit harem-defense behaviors is almost entirely restricted to a relatively small group of prime-aged, harem-holding males that have large bodies and antlers (Clutton-Brock et al. 1988, Pemberton et al. 1992), whereas reproductive success is attributed to a larger group of males possessing a variety of body and horn sizes in bighorn sheep that employ tending, courting, and blocking behaviors (Hogg 1984, Hogg and Forbes 1997).

A tending bond is a mate-guarding behavior where males search out and guard, or tend, individual females that are receptive until breeding is complete or they are displaced by a rival (Hirth 1977, Mooring and Penedo 2014). A number of ungulates are described as primarily using tending-bond behaviors during mate guarding, including moose (*Alces alces*; Bowyer et al. 2011), desert mule deer (*Odocoileus hemionus crooki*; Kucera 1978), American bison (*Bison bison bison*; Roden et al. 2003), eland antelope (*Tragelaphus oryx*; Bro-Jørgensen and Beeston 2015), and white-tailed deer (*Odocoileus virginianus*; Marchington and Hirth 1984). White-tailed deer are the most studied ungulate that primarily employs a tending-bond mating system; however, relatively little is known about factors influencing male reproductive success in this species despite their importance as a game species (DeYoung et al. 2002, 2009; Sorin 2004; Jones et al. 2011; Turner et al. 2016). The peak breeding period for this species typically is short (~3 weeks) in temperate regions of their range, and males tend a single receptive female for 24–48 hours in attempts to secure breeding rights (Knox et al. 1988, Hewitt 2011). The available studies of male breeding success in white-tailed deer have reported that reproduction is spread among a larger group of sires than is typical of ungulates that defend territories or groups of females, presumably because of the obligations of tending and frequently wide distribution of females (Sorin 2004, DeYoung et al. 2009, Turner et al. 2016). Male reproductive success in white-tailed deer has been positively associated with age, with individuals  $\geq 3$  years of age being responsible for the majority of offspring in multiple studies; however, younger males (1.5–2.5 yr) have been reported to make significant reproductive contributions under a variety of demographic conditions (Sorin 2004, DeYoung et al. 2009, Turner et al. 2016). Occurrences of multiple paternity in the same litter have been reported in populations of white-tailed deer, which further supports the concept that a high proportion of males participates in reproduction (DeYoung et al. 2002, Sorin 2004).

Previous investigations of male reproductive success in white-tailed deer have focused almost exclusively on the influence of age (Sorin 2004, DeYoung et al. 2009, Turner et al. 2016). Although insightful, the scope of many of these

studies has been limited by uncertainties associated with field aging techniques that force individuals to be grouped into general age classes (Gee et al. 2002, DeYoung et al. 2009). Further, few studies have considered physical traits (i.e., body size, antler size) that are closely correlated with age, and it is possible that these unmeasured factors are influencing much of the reported positive associations between age and breeding success (Stewart et al. 2000, McElligott et al. 2001, DeYoung et al. 2009, Pelletier and Festa-Bianchet 2006, Jones et al. 2011). A single study of captive deer investigating the role of body mass in male breeding success suggested that body mass, although important, did not fully explain male breeding success in white-tailed deer (Jones et al. 2011). The importance of antlers to male breeding success in white-tailed deer has received scant attention despite the known importance of weaponry in establishing dominance hierarchies and during intraspecific competitions for mates in other ungulate species (Geist 1966, Barrette and Vandal 1990, Andersson 1994, McElligott et al. 1998).

Greater understanding of male reproductive success is of interest from a variety of applied and theoretical perspectives; however, knowledge related to this subject is critically important for management of game species where male harvest often is related to heritable phenotypic traits (Marchington and Hirth 1984, Harris et al. 2002). Prolonged phenotype-based selective harvest of trophy (i.e., possessing large or other highly desirable antler characteristics) males has been linked to declines in genetic diversity and male quality in ungulates (Hartl et al. 1991, Coltman et al. 2003, Pigeon et al. 2016, Pozo et al. 2016), and these findings raise concerns regarding the influence of selective harvest practices on population fitness. Conversely, popular white-tailed deer management practices, including selective harvest (i.e., culling) of inferior (i.e., possessing small or other undesirable antler characteristics) males and selective harvest to promote balanced adult sex ratio and older male age structures (e.g., Quality Deer Management), are often implemented under the expectation that desired demographic conditions will allow older, larger antlered males to have higher reproductive success despite limited evidence in support of these ideas (Woods et al. 1996, Turner et al. 2016). Improved knowledge of patterns of male reproductive success in white-tailed deer would allow for the development of management policies that give greater consideration to long-term genetic implications of selective harvest practices.

We conducted an investigation of the factors influencing male breeding success in an enclosed population of white-tailed deer to better understand reproductive patterns in this species and others with similar breeding ecology. We used genetic-based parentage assignments with detailed information about potential sires, including age, antler size, and body size, to evaluate the relative influences of these factors on annual male breeding success. We conducted this project over multiple years, under a variety of sex ratios and male age structures, which allowed us to simultaneously investigate how changes in demography interacted with male traits to influence annual breeding success.

## STUDY AREA

We conducted this study at Auburn University's Deer Research Facility, which was located in the Piedmont region of east-central Alabama, USA (Neuman et al. 2016). The facility was constructed in October 2007 and consisted of 174 ha enclosed by a 2.6-m steel fence designed to inhibit deer movements. The enclosed population comprised wild animals captured during construction and their descendants. White-tailed deer bred during mid-December to mid-February, with peak conception at approximately January 18. The population size was regulated during the project largely via natural and capture-related mortalities. A number (10–15 individuals) of young-of-the-year deer were captured and released outside the facility at approximately 6 months of age each year to further control deer density and maintain desired numbers of individuals across age classes.

Vegetation was approximately 40% open fields maintained for hay production; 13% bottomland hardwoods (oak [*Quercus* spp.]); 26% mature, naturally regenerated mixed hardwoods (oak and hickory [*Carya* spp.]) and loblolly pine (*Pinus taeda*); 11% early regenerated thicket areas consisting primarily of rose (*Rubus* spp.), sweetgum (*Liquidambar styraciflua*), eastern red cedar (*Juniperus virginiana*), and Chinese privet (*Ligustrum sinense*); and 10% 10–15-year-old loblolly pine. A second-order creek bisected the property and provided a stable source of water year-round. Three feeders provided a 16–18% extruded protein feed (Record Rack<sup>®</sup>, Nutrena Feeds, Minneapolis, MN) available *ad libitum*. Four timed feeders each provided deer approximately 2 kg/day of corn during periods when we were actively capturing deer each year. Two, 0.8-ha fenced plots were planted annually in various warm and cool season forages as part of other ongoing research projects. Deer were allowed to rotationally graze fenced forage plots at regular intervals throughout much of each year as prescribed by projects.

## METHODS

### Field Methods

We chemically immobilized and captured adult ( $\geq 6$  months) deer over 7 trapping seasons (~1 Oct–1 Jul) from 2007–2014. All methods were approved by the Auburn University Institutional Animal Care and Use Committee (2008-1417, 2008-1421, 2010-1785, 2011-1971, and 2013-2372), and followed the American Society of Mammalogists' guidelines (Sikes and Gannon 2011). Deer were immobilized using a combined intramuscular injection of Telazol<sup>®</sup> (Fort Dodge Animal Health, Fort Dodge, IA; 100 mg/ml given at a rate of 4.5 mg/kg) and xylazine (Lloyd Laboratories, Shenandoah, IA; 100 mg/ml given at a rate of 2.2 mg/kg) followed by reversal with the antagonist Tolazine<sup>®</sup> (Lloyd Laboratories; 100 mg/ml given at a rate of 6.6 mg/kg; Miller et al. 2004). We delivered chemical immobilization using cartridge-fired dart guns (Pneu-Dart, Williamsport, PA) equipped with night vision scopes and transmitter darts at feeders (Saalfeld and Ditchkoff 2007).

At initial capture, we recorded sex and aged animals using tooth wear and replacement (Severinghaus 1949). We gave

animals a unique 3-digit identification number that was displayed on visible ear tags and freeze branded individuals on the front shoulder and hind quarter. We took an ear notch sample for genetic analysis and stored samples at  $-78^{\circ}\text{C}$ . We used measurements of chest girth (i.e., measured immediately posterior to the front legs), hind foot length (i.e., the tip of the hoof to the posterior end of the tuber calcis), and body length (i.e., tip of the nose to the base of the tail dorsally hugging the skull and spine) to provide an estimate of body size (Ditchkoff et al. 2001a). We chose not to measure body mass because sampling occurred over prolonged periods that included the breeding season, and body mass is highly variable in male deer during these periods because of increased energy expenditures and fasting associated with breeding activities (Ditchkoff et al. 2001a).

We measured hardened antlers according to the Boone and Crockett scoring system (Nesbitt et al. 2009), which includes measurements of beam and tine length, antler beam circumference, and inside spread between antlers. We did not deduct for differences in antler asymmetry as is standard in net Boone and Crockett scores but rather recorded gross Boone and Crockett score to account for total antler development. Gross Boone and Crockett score is widely accepted as a standard measure of antler development and is an accurate predictor of antler size when using antler mass as standard (Strickland et al. 2013).

Vegetative characteristics and the relatively large size of the facility did not provide an environment where it was possible to view all animals at all times; therefore, we used a combination of methods to estimate deer abundance, adult sex ratio, and age structure. We placed infrared-triggered cameras at feeders and random sites baited with corn during 14 days each February and used the collected images of marked and unmarked deer to estimate deer abundance using mark-recapture methods (Overton 1969, Jacobson et al. 1997). These data were used in conjunction with field observations, and capture and mortality records to determine final population demographic estimates. We considered marked individuals not observed for 2 years to be dead to curb a potentially ever-growing population of dead but unrecovered animals.

### Genetic Analysis and Parentage Assignment

We sent ear notch samples to DNA Solutions (Oklahoma City, OK) for microsatellite analysis of genetic samples for 14 loci (i.e., Cervid1, BM6506, N, INRA011, BM6438, O, BL25, K, Q, D, OarFCB193, P, L, S; Anderson et al. 2002, Meredith et al. 2005). We used FSTAT (Goudet 1995, 2001) to estimate allelic richness (El Mousadik and Petit 1996), gene diversity (Nei 1987), and the inbreeding coefficient ( $F_{IS}$ ; Weir and Cockerham 1984). We used  $F_{IS}$  values to test for possible departures from assumptions regarding Hardy–Weinberg equilibrium (i.e., 1,400 random permutations of alleles) and evaluated genetic disequilibrium among loci (i.e., 9,100 random permutations of genotypes) for the population. We used a Bonferroni correction to correct for multiple comparisons (Rice 1989).

Our sampling methods did not provide us the opportunity to obtain genetic samples from in-utero fetuses or offspring

that perished prior to 6 months of age. Consequently, annual male breeding success in our investigation focused on the number of offspring produced that reached  $\geq 6$  months of age (i.e., recruited individuals). We assigned parentage only to animals initially captured at  $\leq 1.5$  years with a high probability of being aged correctly in an effort to maintain a high level of certainty in offspring cohorts (Gee et al. 2002). We included all deer  $\geq 6$  months of age that were present during each breeding season as candidate parents.

We inserted vaginal implant transmitters (VITs; M3930, Advanced Telemetry Systems, Isanti, MN) in adult females captured after the breeding season during 2010–2013 to facilitate capture of newborn fawns with a known parent (Saalfeld and Ditchkoff 2007). We used these known-parent offspring to blindly validate parentage assignments and empirically verify an assumed genotyping error of 1% (Kalinowski et al. 2007). We excluded neonates captured with the aid of VITs that did not survive to 6 months of age from use in further analyses to maintain consistency in our sampling methods.

We used the likelihood-ratio method in the computer program CERVUS 3.0 to assign parentage using a parent pair analysis (Marshall et al. 1998, Slate et al. 2000, Jones and Arden 2003, Kalinowski et al. 2007). We conducted independent allele frequency analyses and simulations for each of the 6 annual groups of candidate parents and offspring. We used simulations (i.e., 10,000 iterations) to determine critical levels of the delta statistic, which we used to estimate confidence of parentage assignments. We used population demographic parameters in simulations as previously described; however, we conservatively set the proportion of animals sampled at  $\leq 90\%$  for all groups of candidate parents, regardless of estimates, as a precautionary measure to limit inflated reliability of assignments. We assigned parentage to both candidate parents of the most likely parent-offspring trios with  $\leq 4$  mismatching loci when the delta statistic reached a minimum 95% reliability threshold. We also assigned candidate sires paternity in instances where the individual delta statistic reached the 95% level and the pair contained  $\leq 2$  mismatching loci, but the trio failed to reach the 95% level because of mismatches between the dam and offspring.

### Statistical Analyses

The number of annual paternity assignments attributed to individual males during each year of the project represented an individual's annual breeding success. We determined the average age of males  $\geq 6$  months of age in breeding populations for each of the 6 associated breeding seasons, and we used annual mean male age to empirically account for the observed changes in population demographics. We anticipated that changes in important demographic parameters (i.e., deer density, adult sex ratio, and M age structure) would be highly correlated, and we chose male age structure to represent these collective changes in an effort to reduce redundant effects in our models. We used Program R (version 3.0.2, [www.r-project.org](http://www.r-project.org), accessed 1 Mar 2014) to conduct a principal component analysis (PCA) of the 3 body measurements (i.e., chest girth, hind foot length, body length) to generate a single term used to

represent an individual's annual body size; we standardized (i.e., subtracted  $\bar{x}$  and divided by SD) the 3 morphometrics prior to PCA analyses. We used gross Boone and Crockett antler scores to represent an individual's annual antler size, and the known or estimated age of an individual during the corresponding year to represent age; we standardized antler score and age data prior to analyses. We calculated variance inflation factors (VIFs) and pairwise correlation coefficients among age, annual antler size, and annual body size to evaluate collinearity in these data.

We used age, annual antler size, and annual body size to build an *a priori* set of candidate models that reflected biological hypotheses related to their influences on the number of annual paternity assignments attributed to males (Burnham and Anderson 2002). We used drop tests prior to developing our list of models to evaluate support for inclusion of quadratic effects for predictors (Murtaugh 2008). All models included a random term to control for the presence of individual males in the breeding population across multiple years. We also included annual mean male age in all models (except the null model) to account for the observed changes in population demographics. Our set of models were based on the following hypotheses: 1) null model; 2) individual trait models (i.e., no. annual paternity assignments was related to a single measured trait); 3) individual trait  $\times$  demographic models (i.e., no. annual paternity assignments was related to a single measured trait; however, the relationship between the trait and no. annual paternity assignments varied with the observed changes in population demographics); 4) multiple traits models (i.e., no. annual paternity assignments was related to multiple measured traits); 5) multiple traits  $\times$  demographic models (i.e., no. annual paternity assignments was related to multiple measured traits; however, relationships between the traits and no. annual paternity assignments varied along with the observed changes in population demographics).

We used a generalized mixed-effects regression in Program R (package `glmmTMB`) to evaluate candidate models. We tested for the presence of overdispersion in the dataset and selected the appropriate family of error distribution (i.e., Poisson, negative binomial) based upon our findings. We evaluated our data for zero-inflation and selected model specifications accordingly. We used Akaike's Information Criterion adjusted for sample size ( $AIC_c$ ) to rank competitive models, and we considered our most supported models to be those with  $\Delta AIC_c$  values  $\leq 2$  units (Arnold 2010).

## RESULTS

We captured 262 (139 F, 123 M) individual deer during December 2007–March 2014. Collective population monitoring efforts indicated that  $>90\%$  of the adult deer population was captured during the project. Annual breeding populations were largely (50–83%) composed of animals initially captured at  $\leq 2.5$  years of age, resulting in an overall high level of confidence in age estimates. Uncertainties in ages were largely associated with the oldest group of deer that were estimated to be  $>2.5$  years during the 2007–2008 breeding season. Natural mortality of marked adult deer was

**Table 1.** White-tailed deer population demographics by breeding season, Auburn University Captive Deer Research Facility, Alabama, USA.

Metric	2007–2008	2008–2009	2009–2010	2010–2011	2011–2012	2012–2013
Total deer	70	86	100	125	124	119
M	25	40	48	62	67	63
0.5 <sup>a</sup>	11	16	14	21	16	13
1.5	8	10	13	11	12	11
2.5	3	8	9	12	11	9
3.5	3	3	6	8	11	9
4.5	0	3	3	6	8	8
5.5	0	0	3	2	6	7
6.5	0	0	0	2	2	4
7.5	0	0	0	0	1	1
8.5	0	0	0	0	0	1
F	45	46	52	63	57	56
0.5	16	8	14	13	13	10
1.5	7	14	5	14	11	13
2.5	8	5	13	5	9	9
3.5	8	7	5	12	3	3
4.5	4	6	6	5	9	3
5.5	1	4	5	6	4	8
6.5	0	1	2	4	5	4
7.5	1	0	1	2	2	3
8.5	0	1	0	1	1	2
9.5	0	0	1	0	0	1
10.5	0	0	0	1	0	0
Deer/km <sup>2</sup>	40	49	58	72	71	68
Sex ratio (M:F)	1:1.8	1:1.2	1:1.1	1:1.0	1:0.9	1:0.9
$\bar{x}$ M age <sup>b</sup>	1.42	1.68	2.08	2.19	2.81	3.07

<sup>a</sup> Age class (years).

<sup>b</sup> Calculated using males  $\geq 6$  months of age.

low (<10% annually), and there were few (<10% of all captured individuals) instances where we assumed marked deer dead without physical evidence.

Abundances of deer increased over the first 4 years of the study, and then remained relatively constant (Table 1). Adult sex ratio and age structure progressively changed throughout the study to include a greater proportion of males and older individuals. Changes in male age structure were large, with annual mean male age increasing 1.12 times from 2007–2008 to 2012–2013.

We recorded measurements for 120 male deer  $\geq 1.5$  years of age ( $n = 59$  individuals) captured during the project. We captured and measured >50% of potential sires during each year, with the exception of 2007–2008 when we captured 14% of these individuals. In general, antler and body size of males progressively increased with age until 5.5 years, after which they remained relatively constant or slightly declined prior to death (Table 2).

### Parentage Assignment

Evaluation of loci revealed significant departures from Hardy–Weinberg equilibrium at 3 of 14 loci (i.e., Q<sub>1</sub>, D, P) and we removed these loci prior to parentage analysis (Table 3). Of the 11 loci used in parentage analysis, 12 of 55 pairwise comparisons were significant for linkage disequilibrium (loci Cervid and INRA01, Cervid and BL25, Cervid and S, L and INRA01, L and O, L and S, BM6506 and N, BM6438 and N, BL25 and N, K and N, S and N, OAR and S;  $P < 0.05$  after Bonferroni corrections for multiple tests). We retained all remaining 11 loci despite observed genotypic linkages because linkages at this level were not likely to alter

parentage assignments (Sorin 2004). More than 98% of all genotyped individuals had complete genotypes.

We captured 37 known-parent offspring from 24 adult females using VITs during 2010–2013. We assigned maternity to all known-parent offspring at the 95% level, and 36 of 37 were assigned to the correct dam. Mean annual genotyping error in samples from known-parent offspring ( $\bar{x} = 0.011$ , SE = 0.005) was similar to the assumed 1% rate frequently used in simulations.

We assigned paternity at the 95% level to 143 of 157 tested offspring, and most (87%) of these were assigned paternity as part of a parent-pair-offspring trio (Table 4). We assigned paternity to a relatively high proportion of available offspring surviving to  $\geq 6$  months of age during each year of the project according to population estimates ( $\bar{x} = 69 \pm 4.06$  [SE] %). We assigned a parent pair to 27 sets of twins and 2 sets of triplets, and assigned paternity to 2 males in 13 of the 27 sets of twins and 1 of the triplet sets. Multiple males from a wide

**Table 2.** Mean ( $\pm$ SE) gross Boone and Crockett antlers scores (GBCS) and body measurements by age class for male white-tailed deer, Auburn University Deer Research Facility, Alabama, USA, 2007–2013.

Age (yr)	GBCS (cm)			Body length (cm)			Hind foot length (cm)			Chest girth (cm)		
	<i>n</i>	$\bar{x}$	SE	<i>n</i>	$\bar{x}$	SE	<i>n</i>	$\bar{x}$	SE	<i>n</i>	$\bar{x}$	SE
1.5	33	79	4.6	36	128	1.4	36	42	0.3	36	79	0.8
2.5	21	193	8.1	26	139	1.2	26	43	0.3	26	86	1.3
3.5	35	241	6.1	21	149	1.6	21	44	0.3	21	91	1.2
4.5	24	287	7.9	17	151	1.9	17	44	0.4	17	96	1.2
5.5	14	318	8.6	12	151	2.0	12	45	0.4	12	98	1.6
6.5+	10	290	11.2	7	151	3.0	7	43	0.7	7	96	2.3

**Table 3.** White-tailed deer population genetics information, Auburn University Captive Deer Research Facility, Alabama, USA, 2007–2013.

Locus	Samples	Allelic richness	Gene diversity	F <sub>IS</sub>	P <sup>a</sup>
Cervid	261	14	0.879	-0.002	0.585
L	261	9	0.773	-0.001	0.554
BM6506	262	12	0.890	-0.029	0.929
N	262	13	0.875	0.044	0.032
INRA01	262	5	0.322	-0.042	0.846
BM6438	262	9	0.822	0.011	0.376
O	262	8	0.692	-0.031	0.841
BL25	262	5	0.516	0.061	0.091
K	262	4	0.153	-0.022	0.752
Q <sup>b</sup>	261	14	0.842	0.136	<0.001
D <sup>b</sup>	261	10	0.765	0.188	<0.001
OAR	262	12	0.821	-0.013	0.716
P <sup>b</sup>	258	8	0.814	0.176	<0.001
S	262	16	0.895	-0.019	0.854

<sup>a</sup> P value of test for deficit of heterozygotes. Indicative adjusted nominal level (5%) is 0.004.

<sup>b</sup> Loci excluded from parentage analysis because evidence of significant deviance from Hardy–Weinberg equilibrium.

range of available age classes regularly sired offspring, with an average of  $47 \pm 5.18\%$  of candidate sires  $\geq 2.5$  years of age producing offspring on an annual basis (Fig. 1). Although numerous males were responsible for offspring each year, we observed occurrences of high annual reproductive success for select individual males. For example, a 4.5-year-old male fathered 32% of offspring assigned paternity in 2010. Males  $\leq 1.5$  years of age sired 55% of offspring assigned paternity in 2008; however, males of these ages sired relatively fewer offspring in subsequent years ( $\bar{x} = 8 \pm 1.3\%$  of offspring assigned parentage).

### Factors Influencing Annual Male Breeding Success

The PCA analysis of the 3 measured body variables indicated that they were highly correlated; component 1 used to represent annual body size in our analysis accounted for 76.2% of the variance in our data. Estimates of collinearity among age, annual body size, and annual antler size were moderate to high (VIF: sire age = 3.96, body size = 3.14, gross Boone and Crockett antler score = 5.98).

Drop tests indicated support for inclusion of a quadratic effort for age in our set of candidate models; however, results did not support inclusion of quadratic effects for body size or antler score as evidenced by AIC<sub>c</sub> scores (Table 5). We found evidence of slight overdispersion in our dataset when testing

**Table 4.** Summary of annual sampling of white-tailed deer offspring, Auburn University Deer Research Facility, Alabama, 2007–2013.

Year	Estimated <sup>a</sup>	Tested <sup>b</sup>	Assigned <sup>c</sup>
2007–2008	28	22	20
2008–2009	30	24	24
2009–2010	40	30	28
2010–2011	36	28	19
2011–2012	33	30	25
2012–2013	44	32	27

<sup>a</sup> Number of estimated offspring according to monitoring efforts as of 1 March 2016.

<sup>b</sup> Number of known-age individuals tested for parentage.

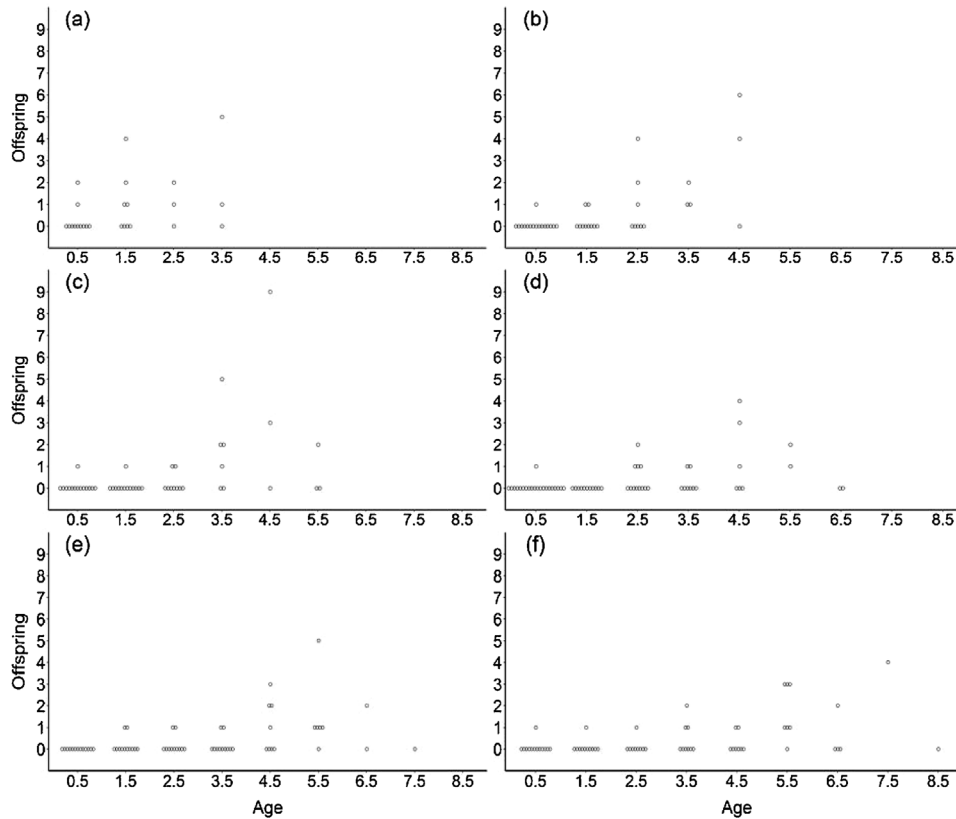
<sup>c</sup> Number of tested offspring assigned paternity at 95% level.

our global model with a Poisson distribution (Pearson statistic: residual degrees of freedom = 1.68). In consideration to these findings, we used negative binomial distributions for all tested models. The fit of the global model (AIC<sub>c</sub> = 213.1) was not improved by accounting for zero-inflation (AIC<sub>c</sub> = 215.1) and, as such, we did not address zero-inflation in our models.

Our most supported model (model 19) indicated that annual body size and annual antler size were positively associated with annual male breeding success (Tables 6 and 7; Figs. 2 and 3). The relationship between annual antler size and annual male breeding success varied along with the observed changes in annual male mean age (our covariate representing population structure). Our findings suggested that lower deer density, female-skewed sex ratios, and younger male age structures provided increased opportunities for males of all antler sizes to reproduce, whereas reproduction was largely limited to males with the largest antlers under opposing demographic conditions. In one of the additional highly supported models (model 3), body size remained influential to annual male breeding success, but the effects of annual antler size were not included in the model. The final highly supported model (model 10) attributed annual male breeding success to annual body size and annual antler size; however, there was no evidence that effects of these predictors were influenced by the observed changes in demographics.

## DISCUSSION

Although age, antler size, and body size were, as expected, highly collinear for males in the study population, our analyses provided insight into the relative importance of these factors as determinants of reproductive success. Multicollinearity among predictors can overinflate the standard errors of the coefficients, making it difficult to determine their importance (Graham 2003); however, multicollinearity in our data did not appear to be problematic in our analyses. Our results demonstrated that annual reproductive success was positively related to the body size and antler size of male white-tailed deer. Body size has been identified as a reliable predictor of male reproductive effort in numerous ungulate species (Clutton-Brock et al. 1988, Pélabon et al. 1999, McElligott et al. 2001, Mysterud et al. 2004, Johnson et al. 2007). In species, such as white-tailed deer, where males greatly reduce food intake during the breeding season and actively pursue and tend females for prolonged periods of time, large body size could provide significant competitive advantages. Males with larger body size are capable of storing greater amounts of total energy reserves than smaller counterparts and an increasing proportion of body mass is stored as fat (Lindstedt and Boyce 1985). The large volume of high quality energy reserves may help these individuals maintain good body condition, which in turn may positively affect social dominance, reproductive effort, and ultimately reproductive success. Large body size may also positively affect male reproductive success in white-tailed deer via post-copulatory competitive advantages because sperm volume per ejaculate has been directly related to body size in other species (Møller 1991). Post-copulatory



**Figure 1.** Strip plots of annual number of offspring produced by individual white-tailed deer males in relation to age for the 2007–2008 (a), 2008–2009 (b), 2009–2010 (c), 2010–2011 (d), 2011–2012 (e), and 2012–2013 (f) breeding seasons, Auburn University Deer Research Facility, Alabama, USA.

**Table 5.** Candidate models used to investigate relationships between number of annual paternity assignments for individual white-tailed deer and male age, annual antler size, and annual body size, Auburn University Captive Deer Research Facility, Alabama, USA, 2007–2013.

Model category	Model	Parameters <sup>a</sup>
Null	1	1 + R
Individual trait	2	Age <sup>2</sup> + M + R
	3	Body + M + R
	4	Antler + M + R
Individual trait × demographic	5	Age <sup>2</sup> + age <sup>2</sup> × M + M + R
	6	Body + body × M + M + R
	7	Antler + antler × M + M + R
Multiple traits	8	Age <sup>2</sup> + body + M + R
	9	Age <sup>2</sup> + antler + M + R
	10	Body + antler + M + R
Multiple traits × demographic	11	Age <sup>2</sup> + body + antler + M + R
	12	Age <sup>2</sup> + body + age <sup>2</sup> × M + M + R
	13	Age <sup>2</sup> + body + body × M + M + R
	14	Age <sup>2</sup> + body + body × M + age <sup>2</sup> × M + M + R
	15	Age <sup>2</sup> + antler + age <sup>2</sup> × M + M + R
	16	Age <sup>2</sup> + antler + antler × M + M + R
	17	Age <sup>2</sup> + antler + age <sup>2</sup> × M + antler × M + M + R
	18	Body + antler + body × M + M + R
	19	Body + antler + antler × M + M + R
	20	Body + antler + body × M + antler × M + M + R
	21	Age <sup>2</sup> + body + antler + age <sup>2</sup> × M + M + R
	22	Age <sup>2</sup> + body + antler + body × M + M + R
	23	Age <sup>2</sup> + body + antler + antler × M + M + R
	24	Age <sup>2</sup> + body + antler + age <sup>2</sup> × M + body × M + M + R
	25	Age <sup>2</sup> + body + antler + age <sup>2</sup> × M + antler × M + M + R
	26	Age <sup>2</sup> + body + antler + body × M + antler × M + M + R
	27	Age <sup>2</sup> + body + antler + age <sup>2</sup> × M + body × M + antler × M + M + R

<sup>a</sup> Parameters include annual body size (body), annual antler size (antler), annual mean male age of the herd (M), and a random term for individual males (R). Linear and quadratic effects are included wherever age<sup>2</sup> is used.

**Table 6.** Candidate model selection results for examination of relationships between number of annual paternity assignments for individual white-tailed deer and male age, annual antler size, and annual body size, Auburn University Captive Deer Research Facility, Alabama, USA, 2007–2013. We present only the null model and those with corrected Akaike’s Information Criterion (AIC<sub>c</sub>) weight ( $w_i$ )  $\geq 0.05$ .

Model	Parameters <sup>a</sup>	df	$\Delta AIC_c$	$w_i$
19	Body + antler + antler $\times$ M + M + R	7	0.00	0.23
3	Body + M + R	5	0.70	0.16
10	Body + antler + M + R	6	1.30	0.12
20	Body + antler + body $\times$ M + antler $\times$ M + M + R	8	2.10	0.08
6	Body + body $\times$ M + M + R	6	2.50	0.06
18	Body + antler + body $\times$ M + M + R	7	2.70	0.06
8	Age <sup>2</sup> + body + M + R	7	2.80	0.05
1	1 + R	2	125.43	0.00

<sup>a</sup> Parameters include annual body size (body), annual antler size (antler), annual mean male age of the herd (M), and a random term for individual males (R). Linear and quadratic effects are included wherever age<sup>2</sup> is used.

advantages may be of particular importance to white-tailed deer given the relatively high rates of multiple paternity (i.e., offspring in a litter are attributed to  $>1$  M) reported in this and other captive studies (Sorin 2004, DeYoung et al. 2006). Although female mate choice generally is poorly understood, female preference of large-bodied males is an additional possible explanation for high reproductive success for this group of males (Clutton-Brock et al. 1989, Byers et al. 1994).

The evolution and persistence of nutritionally costly secondary sexual characteristics in male ungulates inherently implies an associated reproductive advantage (Geist 1966, Johnson et al. 2007). Antler size is recognized by male ungulates and affects behavior (Bubenik 1983), and our results indicate that antler size played a role in determining annual male reproductive success in white-tailed deer. However, our findings indicated that the strength of the positive relationship between antler size and annual reproductive success was sensitive to herd characteristics, with antler size gaining importance as male age structure shifted to contain greater numbers of older males. Antlers serve a variety of purposes in male reproduction, including weaponry during direct intraspecific competition for access to females (Andersson 1994) and visual cues used to assess rival males prior to direct confrontations (Clutton-Brock 1979, McElligott et al. 1998). The competitive environment for access to females is shaped by deer abundance and male age structure (Clutton-Brock et al. 1997, DeYoung et al.

2009, Martin et al. 2016), and it is possible that female-skewed adult sex ratios and relatively young male age structures present during the early years of the project provided an environment of low contest competition among males for mates, thereby diminishing the role of antler size in male reproductive success. Young males of many ungulate species favor reproductive tactics that are less reliant upon exertion of physical dominance, such as sneaking (kleptogony) and courting (Sinervo and Lively 1996, Hogg and Forbes 1997, Sorin 2004, Isvaran 2005, Willis et al. 2012), and, as such, the role of antlers, and other weaponry, in reproduction may be diminished when females are readily available and most potential sires do not favor fighting tactics during reproductive efforts. Conversely, the abundance of prime males and the balanced to male-skewed sex ratios observed during later years in this study likely provided an environment of intense contest competition for breeding opportunities, which may have resulted in an increased importance of antler size under these conditions.

Our findings regarding the relative importance of body size and antler size to male reproductive success in white-tailed deer are supported by findings in other polygynous ungulate species (Andersson 1994, Coltman et al. 1999, McElligott et al. 2001, Pelletier and Festa-Bianchet 2006). For example, antler breakage in tule elk (*Cervus elaphus nannodes*) had no effect on male–male assessment, fighting success, or harem-holding status (Johnson et al. 2007), which is contrary to what would be expected if antler characteristics were a robust determinant of male reproduction. Studies of bighorn sheep demonstrated that horn length was of little importance to reproductive success for subordinate males that primarily acquired breeding opportunities via courting tactics but became increasingly important for older males that frequently used tending behaviors (Hogg and Forbes 1997, Coltman et al. 2002). Large body size might have been a more consistent predictor of reproductive success than antler size in our study because large physical size conferred reproductive advantages, not only for males that gained breeding opportunities through contest competitions but also to those using alternative tactics. Endurance is important to reproductive success for males using searching and courting tactics to acquire breeding opportunities, and large body size would logically allow for these individuals to store more energy reserves for these activities (Hogg 1984,

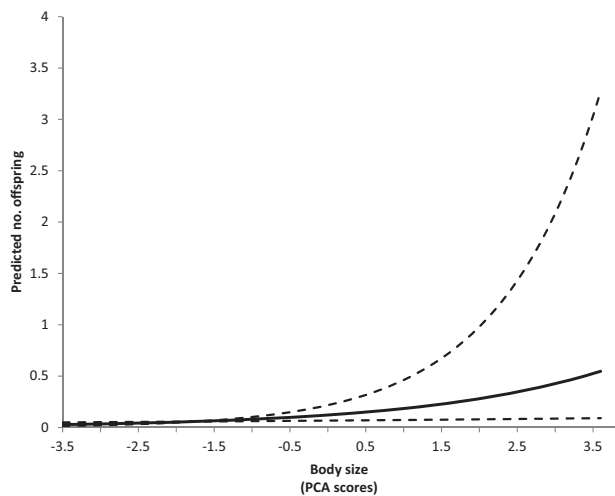
**Table 7.** Summary of fixed effect estimates for supported models (difference in corrected Akaike’s Information Criterion [ $\Delta AIC_c$ ]  $\leq 2.0$ ) of male white-tailed deer reproduction, Auburn University Captive Deer Research Facility, Alabama, USA, 2007–2013.

Model	AIC <sub>c</sub>	Parameters <sup>a</sup>	$\beta$	SE	$P^b$
19	205.9	Body	1.52	1.19	0.014
		Antler	1.72	1.35	0.706
		M	–1.66	1.21	0.008
		Antler $\times$ M	1.37	1.17	0.045
3	206.6	Body	1.87	1.13	$<0.001$
		M	–1.26	1.15	0.094
10	207.2	Body	1.56	1.20	0.014
		Antler	1.43	1.33	0.206
		M	–1.36	1.17	0.048

<sup>a</sup> Parameters include annual body size (body), annual antler size (antler), and annual mean male age of the herd (M).

<sup>b</sup> Alpha value for significance = 0.05.



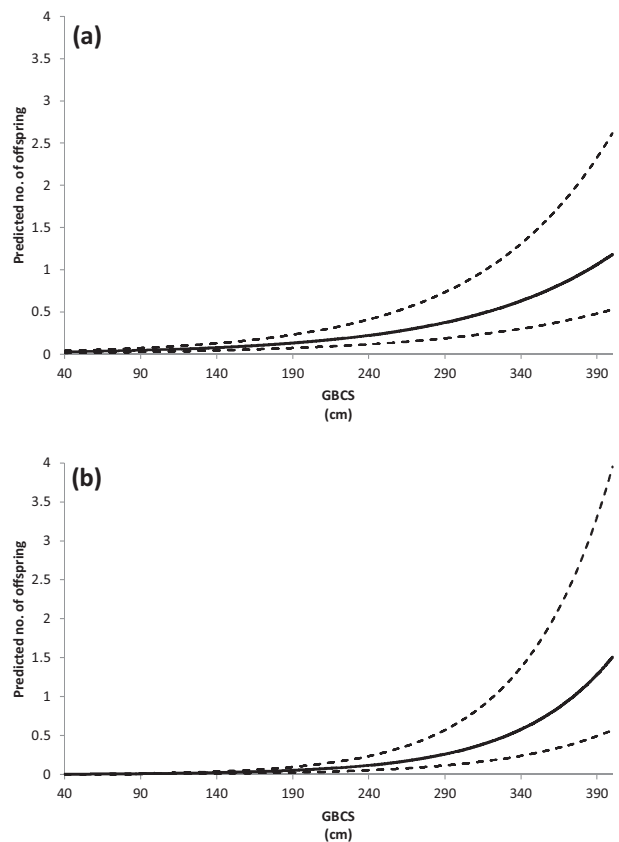


**Figure 2.** Predicted relationship between male white-tailed deer body size (principal component analysis [PCA] scores = body length, chest girth, hind foot length) and annual number of offspring at an annual average male age of 2.16 years and gross Boone and Crockett antler score (GBCS) of 220 cm, Auburn University Deer Research Facility, Alabama, USA, 2007–2013. We determined estimates using a generalized linear mixed model with negative binomial distribution. Values of average male age and GBCS used in the predictive model represented mean observed values. Dashed lines indicate 95% confidence interval.

Lindstedt and Boyce 1985). Alternatively, antler size may only provide significant reproductive advantages for males that use fighting tactics to control access to mates, or if a preference for large antler males exists among females.

Age frequently has been used to group candidate sires when evaluating male breeding success because of the relative ease of collecting age data and large volume of reported information describing positive relationships between age, dominance status, and reproductive success (Owen-Smith 1993, Komers et al. 1997, Ditchkoff et al. 2001b, DeYoung et al. 2009, Willisich and Neuhaus 2010). Age may also be used as a surrogate for other behavioral factors, such as experience (Jones et al. 2011). Research suggests that factors that are highly correlated with age (e.g., body and antler size) may account for much of the positive relationship between age and male reproductive success in ungulates (McElligott et al. 2001). Our top supported models did not include age as a factor influencing male breeding success in the study population, which lends further credibility to the idea that the physical correlates of age are influencing the reported associations. The lack of a significant relationship between age and male breeding success after controlling for important physical correlates also suggests that age-related experience did not play a large role in determining annual male reproduction in our herd. Nonetheless, age remains useful as a broad means for evaluating male reproductive potential in circumstances where measurements of correlated physical variables are not possible, so long as limitations to inferences are acknowledged.

Previous research has suggested that highly synchronous estrous and wide spatial distribution of female white-tailed deer creates an environment where it is difficult for a specific age class of males, let alone individuals, to monopolize breeding (DeYoung et al. 2009, Turner et al.



**Figure 3.** Predicted relationship between male white-tailed deer antler size (i.e., gross Boone and Crockett antler score [GBCS]) and annual number of offspring at annual average male ages of 1.42 years (a) and 3.07 years (b), Auburn University Deer Research Facility, Alabama, USA, 2007–2013. Values of annual average male age represent the minimum and maximum observed in the population during the project. We determined estimates using a generalized linear mixed model with a negative binomial distribution. Body size was fixed at the mean observed value for the predictive model. Dashed lines indicate 95% confidence interval.

2016). Life-history theory suggests that age-related reproductive effort is dependent upon growth and survival, with age at first reproduction being younger for fast growth-low survival species than slow growing-longer lived species (Stearns 1992). White-tailed deer are considered to have faster growth and lower annual survival than many other large mammals, and as such reproductive effort in young males is predicted to be higher than in slower growing-longer lived ungulates (e.g., red deer; Geist 1998, Nussey et al. 2009, Festa-Bianchet 2012, Willisich et al. 2012). We observed patterns of reproductive success in agreement with these theories in the studied population, with numerous males of all ages, including young-of-the-year, successfully producing offspring across a range of herd characteristics. These findings logically support the concept that male white-tailed deer employ multiple mating tactics, including but not limited to tending, to successfully secure breeding opportunities, and the adopted mating tactics may be age dependent as demonstrated in other ungulates (Hogg and Forbes 1997, Coltman et al. 2002, Willisich et al. 2012). Female-skewed sex ratios and young male age structures appeared to provide increased breeding opportunities for

subordinate males likely using alternative mating tactics, presumably because of relatively low encounter rates among competitors (Crowley et al. 1991). Reproductive success was reduced for young males under conditions where prime-aged males were more abundant and sex ratios were more balanced, likely as a result of increased levels of contest competition for mates. Sexual selection intensity is directly related to the competitive environment, and our results provide some evidence that the intensity of competition, and consequently sexual selection, may have been greater under demographic conditions where prime competitors were more abundant (Martin et al. 2016). These results have important implications for management of game species (e.g., white-tailed deer) that are often selectively harvested on the basis of heritable phenotypic traits (Myserud 2011, Pigeon et al. 2016). Management for demographic conditions where prime-aged males are relatively abundant and sex ratios are balanced may contribute to the promotion of desirable sexually selected traits through increased male contest competitions; however, these effects are likely moderated in species such as white-tailed deer where annual reproduction is distributed among a relatively large proportion of males across a range of demographic conditions.

Previous research of a free ranging white-tailed deer population in South Carolina reported that 28% of male fawns were sexually mature (Peles et al. 2000), and a minimum of 12.5% of captive male fawns successfully bred in a study conducted in Louisiana (Schultz and Johnson 1992); however, breeding by young-of-the-year males in our study represents, to our knowledge, the first documented occurrence of male white-tailed deer fawns breeding in a semi-natural environment. Although breeding by male fawns is a known possibility, the implications of our findings prompted us to more critically investigate the events. The 2 most likely scenarios that could result in a male fawn erroneously being assigned as a sire would occur if the male fawn is the offspring of a true father, and the true father is not included as a candidate sire, or the male fawn is a previous-litter full sibling of the tested offspring (Jones and Arden 2003). The first scenario is unlikely because paternities had been assigned for all fawn sires, and we excluded the fathers of male fawn sires in the assignments. We reviewed our parentage assignments to determine if fawn sires and associated offspring shared a dam in an effort to investigate the potential for the second presented source of error. We found no evidence for errors of this type; none of the fawn sires and associated offspring shared a dam. We acknowledge the potential for some of the identified breeding by male fawns to be the result of analytical errors; however, the conservative methods used to assign parentage and high level of sampling of candidate parents limited these errors and support our finding that male fawns participated in breeding over the course of the study.

Peles et al. (2000) reported that body mass and kidney fat index were positively associated with presence of testicular spermatozoa in fawns, which indicates that overall condition may be important in timing of puberty in male fawns. Body condition influences reproductive rates in female fawns (Sauer 1984), and a study conducted under relatively similar

conditions reported that young male white-tailed deer mated almost exclusively with young females (Sorin 2004). Our findings were similar within the 2 known-age parent pairs where a male fawn was identified as the sire, with the parent pairs consisting of a male and female fawn in one instance and a male fawn and yearling female in the other. High quality natural and planted forages and supplemental feed were available to deer in our study year-round, providing an environment where puberty in young deer was under little, if any, immediate nutritional constraints. Consequently, results from our study related to reproductive success of male fawns may not accurately reflect patterns of reproduction in environments with greater nutritional limitations.

We observed relatively high rates of polyandry during the study, further verifying that multiple paternities occur in this species and are common across a range of demographic conditions. Various ideas have been proposed to account for polyandry in white-tailed deer, including sneaking of males while the initial tending male is warding off competitors, failure of sires to tend a female the entire duration of estrus, and female behavior related to mate choice (Clutton-Brock et al. 1979, Sinervo and Lively 1996). Perhaps the most widely accepted explanation for multiple paternities is a displacement hypothesis, where a younger male tending a receptive female is displaced by a more dominant male (Marchington and Hirth 1984). Twelve of the 13 instances of multiple paternity identified in our study involved males with  $\geq 1$  year difference in estimated ages, which may lend support to the displacement of young males by older, more dominant males as a plausible mechanism; however, it is difficult to determine if these patterns were attributed to chance alone because the group of breeding males was extremely diverse in terms of age.

## MANAGEMENT IMPLICATIONS

Our study highlights the importance of body size and antler size to male reproductive success in white-tailed deer, with antler size playing an increasingly important role as the herd shifted to contain a balanced adult sex ratio and older male age structure. Reproduction was not, however, monopolized by the group of males with the largest antler and body size under any of the observed conditions. Age-related reproductive skew was influenced by herd demographics, with young males being responsible for more offspring under the most female-biased sex ratios and youngest male age structures. Our results imply that management practices that promote balanced adult sex ratios and older male age structures (e.g., Quality Deer Management) may foster a highly competitive environment where breeding by younger and smaller antlered males is under greater restrictions. As a result, the intensity of sexual selection in male white-tailed deer is potentially increased under these management practices, which may have positive long-term genetic implications for heritable phenotypic traits. However, the genetic effects, whether positive or negative, of selective harvest will likely be limited in species such as white-tailed deer where reproductive success frequently is attributed to a high proportion of males.

## ACKNOWLEDGMENTS

We thank the large team of volunteers who assisted in data collection and V. Jackson for assisting with maintenance of the facility. We thank the Center for Forest Sustainability at Auburn University, Code Blue Scents, Moultrie, EBSCO Industries, Nutrena Feeds, and other individuals who provided private financial support.

## LITERATURE CITED

- Anderson, J. D., R. L. Honeycutt, R. A. Gonzales, K. L. Gee, L. C. Skow, R. L. Gallagher, D. A. Honeycutt, and R. W. DeYoung. 2002. Development of microsatellite DNA markers for the automated genetic characterization of white-tailed deer populations. *Journal of Wildlife Management* 66:67–74.
- Andersson, M. B. 1994. *Sexual selection*. Princeton University Press, Princeton, New Jersey, USA.
- Arnold, T. W. 2010. Uninformative parameters and model selection using Akaike's Information Criterion. *Journal of Wildlife Management* 74:1175–1178.
- Barrette, C., and D. Vandal. 1990. Sparring, relative antler size, and assessment in male caribou. *Behavioral Ecology and Sociobiology* 26:383–387.
- Bowyer, R. T., J. L. Rachlow, K. M. Stewart, and V. Van Ballenberghe. 2011. Vocalizations by Alaskan moose: female incitation of male aggression. *Behavioral Ecology and Sociobiology* 65:2251–2260.
- Bro-Jørgensen, J., and J. Beeston. 2015. Multimodal signalling in an antelope: fluctuating facemasks and knee-clicks reveal the social status of eland bulls. *Animal Behaviour* 102:231–239.
- Bubenik, A. B. 1983. The behavioral aspects of antlerogenesis. Pages 389–449 in R. D. Brown, editor. *Antler development in Cervidae*. Caesar Kleberg Wildlife Research Institute, Kingsville, Texas, USA.
- Burnham, K. P., and D. R. Anderson. 2002. *Model selection and multimodel inference: a practical information-theoretic approach*. Springer Science & Business Media, New York, New York, USA.
- Byers, J. A., J. D. Moodie, and N. Hall. 1994. Pronghorn females choose vigorous mates. *Animal Behaviour* 47:33–43.
- Ciuti, S., and M. Apollonio. 2016. Reproductive timing in a lekking mammal: male fallow deer getting ready for female estrus. *Behavioral Ecology* 27:1522–1532.
- Clutton-Brock, T. H. 1979. The functions of antlers. *Behavior* 79:108–125.
- Clutton-Brock, T. H. 1989. Review lecture: mammalian mating systems. *Proceedings of the Royal Society of London B: Biological Sciences* 236:339–372.
- Clutton-Brock, T. H., S. D. Albon, R. M. Gibson, and F. E. Guinness. 1979. The logical stag: adaptive aspects of fighting in red deer (*Cervus elaphus*). *Animal Behaviour* 27:211–225.
- Clutton-Brock, T. H., S. D. Albon, and F. E. Guinness. 1988. Reproductive success in male and female red deer. Pages 325–343 in T. H. Clutton-Brock, editor. *Reproductive success: studies of individual variation in contrasting breeding systems*. University of Chicago Press, Chicago, Illinois, USA.
- Clutton-Brock, T. H., M. Hiraiwa-Hasegawa, and A. Robertson. 1989. Mate choice on fallow deer leks. *Nature* 340:463–465.
- Clutton-Brock, T. H., K. E. Rose, and F. E. Guinness. 1997. Density-related changes in sexual selection in red deer. *Proceedings of the Royal Society of London B: Biological Sciences* 264:1509–1516.
- Coltman, D. W., D. R. Bancroft, A. Robertson, J. A. Smith, T. H. Clutton-Brock, and J. M. Pemberton. 1999. Male reproductive success in a promiscuous mammal: behavioural estimates compared with genetic paternity. *Molecular Ecology* 8:1199–1209.
- Coltman, D. W., M. Festa-Bianchet, J. T. Jorgenson, and C. Strobeck. 2002. Age-dependent sexual selection in bighorn rams. *Proceedings of the Royal Society of London B: Biological Sciences* 269:165–172.
- Coltman, D. W., P. O'Donoghue, J. T. Jorgenson, J. T. Hogg, C. Strobeck, and M. Festa-Bianchet. 2003. Undesirable evolutionary consequences of trophy hunting. *Nature* 426:655–658.
- Crowley, P. H., S. E. Travers, M. C. Linton, S. L. Cohn, A. Sih, and R. C. Sargent. 1991. Mate density, predation risk, and the seasonal sequence of mate choices: a dynamic game. *American Naturalist* 137:567–596.
- DeYoung, R. W., S. Demarais, K. L. Gee, R. L. Honeycutt, M. W. Hellickson, 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.
- DeYoung, R. W., S. Demarais, R. L. Honeycutt, K. L. Gee, and R. A. Gonzales. 2006. Social dominance and male breeding success in captive white-tailed deer. *Wildlife Society Bulletin* 34:131–136.
- Ditchkoff, S. S., R. L. Lochmiller, R. E. Masters, S. R. Hooper, and R. A. V. D. Bussche. 2001a. Major-histocompatibility-complex-associated variation in secondary sexual traits of white-tailed deer (*Odocoileus virginianus*): evidence for good-genes advertisement. *Evolution* 55:616–625.
- Ditchkoff, S. S., E. R. Welch Jr., R. L. Lochmiller, R. E. Masters, and W. R. Starry. 2001b. Age-specific mortality of adult, male white-tailed deer supports mate competition theory. *Journal of Wildlife Management* 65:552–559.
- El Mousadik, A., and R. 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.
- Festa-Bianchet, M. 2012. The cost of trying: weak interspecific correlations among life-history components in male ungulates. *Canadian Journal of Zoology* 90:1072–1085.
- Gee, K. L., J. H. Holman, M. K. Causey, A. N. Rossi, and J. B. Armstrong. 2002. Aging white-tailed deer by tooth wear: a critical evaluation of a time-honored technique. *Wildlife Society Bulletin* 30:387–393.
- Geist, V. 1966. The evolution of horn-like organs. *Behavior* 27:175–214.
- Geist, V. 1998. *Deer of the world: their evolution, behavior, and ecology*. Stackpole Books, Harrisburg, Pennsylvania, USA.
- Gosden, T. P., and E. I. Svensson. 2008. Spatial and temporal dynamics in a sexual selection mosaic. *Evolution* 62:845–856.
- Goudet, J. 1995. FSTAT (version 1.2): a computer program to calculate F-statistics. *Journal of Heredity* 86:485–486.
- Goudet, J. 2001. FSTAT: a computer program to estimate and test gene diversities and fixation indices (version 2.9.3.). Lausanne University, Lausanne, Switzerland.
- Graham, M. H. 2003. Confronting multicollinearity in ecological multiple regression. *Ecology* 84:2809–2815.
- Harris, R. B., W. A. Wall, and F. W. Allendorf. 2002. Genetic consequences of hunting: What do we know and what should we do? *Wildlife Society Bulletin* 30:634–643.
- Hartl, G. B., G. Lang, F. Klein, and R. Willing. 1991. Relationships between allozymes, heterozygosity and morphological characters in red deer (*Cervus elaphus*), and the influence of selective hunting on allele frequency distributions. *Heredity* 66:343–350.
- Hendrick, A. V., and E. J. Temeles. 1989. The evolution of sexual dimorphism in animals: hypotheses and tests. *Trends in Ecology and Evolution* 4:136–138.
- Hewitt, D. G. 2011. *Biology and management of white-tailed deer*. CRC Press, Boca Raton, Florida, USA.
- Hirth, D. H. 1977. Social behavior of white-tailed deer in relation to habitat. *Wildlife Monographs* 53:1–55.
- Hogg, J. T. 1984. Mating in bighorn sheep: multiple creative male strategies. *Science* 225:526–529.
- Hogg, J. T. 1987. Intrasexual competition and mate choice in Rocky Mountain bighorn sheep. *Ethology* 75:119–144.
- Hogg, J. T., and S. H. Forbes. 1997. Mating in bighorn sheep: frequent male reproduction via a high-risk “unconventional” tactic. *Behavioral Ecology and Sociobiology* 41:33–48.
- Isvaran, K. 2005. Variation in male mating behaviour within ungulate populations: patterns and processes. *Current Science* 89:1192–1199.
- 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.
- Johnson, H., V. Bleich, P. Krausman, and J. Koprowski. 2007. Effects of antler breakage on mating behavior in male tule elk (*Cervus elaphus nannodes*). *European Journal of Wildlife Research* 53:9–15.
- Jones, A. G., and W. R. Arden. 2003. Methods of parentage analysis in natural populations. *Molecular Ecology* 12:2511–2523.
- 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.

- Knox, W. M., K. V. Miller, and R. L. Marchinton. 1988. Recurrent estrous cycles in white-tailed deer. *Journal of Mammalogy* 69:384–386.
- Komers, P. E., C. Pélabon, and D. Stenström. 1997. Age at first reproduction in male fallow deer: age-specific versus dominance-specific behaviors. *Behavioral Ecology* 8:456–462.
- Kruuk, L. E., T. Clutton-Brock, and J. M. Pemberton. 2014. Case study: quantitative genetics and sexual selection of weaponry in a wild ungulate. Pages 160–176 in A. Charmantier, D. Garant, and L. E. B. Kruuk, editors. *Quantitative genetics in the wild*. Oxford University Press, Oxford, United Kingdom.
- Kruuk, L. E. B., J. Slate, J. M. Pemberton, S. Brotherstone, F. Guinness, and T. Clutton-Brock. 2002. Antler size in red deer: heritability and selection but no evolution. *Evolution* 56:1683–1695.
- Kucera, T. E. 1978. Social behavior and breeding system of the desert mule deer. *Journal of Mammalogy* 59:463–476.
- Lindstedt, S. L., and M. S. Boyce. 1985. Seasonality, fasting endurance, and body size in mammals. *American Naturalist* 125:873–878.
- Marchington, R. L., and D. H. Hirth. 1984. *White-tailed deer: ecology and management*. Stackpole Books, Harrisburg, Pennsylvania, USA.
- Marino, A. 2012. Indirect measures of reproductive effort in a resource-defense polygynous ungulate: territorial defense by male guanacos. *Journal of Ethology* 30:83–91.
- Marshall, T., J. Slate, L. Kruuk, and J. Pemberton. 1998. Statistical confidence for likelihood-based paternity inference in natural populations. *Molecular Ecology* 7:639–655.
- Martin, A. M., M. Festa-Bianchet, D. W. Coltman, and F. Pelletier. 2016. Demographic drivers of age-dependent sexual selection. *Journal of Evolutionary Biology* 29:1437–1446.
- McElligott, A. G., M. P. Gammell, H. C. Harty, D. R. Paini, D. T. Murphy, J. T. Walsh, and T. J. Hayden. 2001. Sexual size dimorphism in fallow deer (*Dama dama*): do larger, heavier males gain greater mating success? *Behavioral Ecology and Sociobiology* 49:266–272.
- McElligott, A. G., V. Mattiangeli, S. Mattiello, M. Verga, C. A. Reynolds, and T. J. Hayden. 1998. Fighting tactics of fallow bucks (*Dama dama*, Cervidae): reducing the risks of serious conflict. *Ethology* 104:789–803.
- Meredith, E., J. Rodzen, K. Levine, and J. Banks. 2005. Characterization of an additional 14 microsatellite loci in California elk (*Cervus elaphus*) for use in forensic and population applications. *Conservation Genetics* 6:151–153.
- 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/xyzazine immobilization in female white-tailed deer. *Journal of Wildlife Diseases* 40:533–537.
- Møller, A. P. 1991. Concordance of mammalian ejaculate features. *Proceedings of the Royal Society of London. Series B: Biological Sciences* 246:237–241.
- Mooring, M. S., and M. C. T. Penedo. 2014. Behavioral versus genetic measures of fitness in bison bulls (*Bison bison*). *Journal of Mammalogy* 95:913–924.
- Murtaugh, P. A. 2008. Performance of several variable-selection methods applied to real ecological data. *Ecology Letters* 12:1061–1068.
- Mysterud, A. 2011. Selective harvesting of large mammals: how often does it result in directional selection? *Journal of Applied Ecology* 48:827–834.
- Mysterud, A., O. Y. Holand, K. H. Røed, H. Gjøstein, J. Kumpula, and M. Nieminen. 2003. Effects of age, density, and sex ratio on reproductive effort in male reindeer (*Rangifer tarandus*). *Journal of Zoology* 261:341–344.
- Mysterud, A., R. Langvatn, and N. C. Stenseth. 2004. Patterns of reproductive effort in male ungulates. *Journal of Zoology* 264:209–215.
- Nei, M. 1987. *Molecular evolutionary genetics*. Columbia University Press, New York, New York, USA.
- Nesbitt, W. H., P. L. Wright, E. L. Buckner, C. R. Byers, and J. Reneau. 2009. *Measuring and scoring North American big game trophies*. 3 edition. Boone and Crockett Club, Missoula, Montana, USA.
- Neuman, T. J., C. H. Newbolt, S. S. Ditchkoff, and T. D. Steury. 2016. Microsatellites reveal plasticity in reproductive success of white-tailed deer. *Journal of Mammalogy* 97:1441–1450.
- Nussey, D. H., L. E. Kruuk, A. Morris, M. N. Clements, J. M. Pemberton, and T. H. Clutton-Brock. 2009. Inter- and intrasexual variation in aging patterns across reproductive traits in a wild red deer population. *American Naturalist* 174:342–357.
- Overton, W. S. 1969. *Estimating the numbers of animals in wildlife populations*. Third edition. The Wildlife Society, Washington, D.C., USA.
- Owen-Smith, N. 1993. Age, size, dominance, and reproduction among male kudus: mating enhancement by attrition of rivals. *Behavioral Ecology and Sociobiology* 32:177–184.
- Pélabon, C., P. E. Komers, B. Birgersson, and K. Ekvall. 1999. Social interactions of yearling male fallow deer during rut. *Ethology* 105:247–258.
- 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.
- Pelletier, F., and M. Festa-Bianchet. 2006. Sexual selection and social rank in bighorn rams. *Animal Behaviour* 71:649–655.
- Pemberton, J. M., S. D. Albon, F. E. Guinness, T. H. Clutton-Brock, and G. A. Dover. 1992. Behavioral estimates of male mating success tested by DNA fingerprinting in a polygynous mammal. *Behavioral Ecology* 3:66–75.
- Pigeon, G., M. Festa-Bianchet, D. W. Coltman, and F. Pelletier. 2016. Intense selective hunting leads to artificial evolution in horn size. *Evolutionary Applications* 9:521–530.
- Pozo, R. A., S. Schindler, S. Cubaynes, J. J. Cusack, T. Coulson, and A. F. Malo. 2016. Modeling the impact of selective harvesting on red deer antlers. *Journal of Wildlife Management* 80:978–989.
- Rice, W. R. 1989. Analyzing tables of statistical tests. *Evolution* 43:223–225.
- Roden, C., V. Hilde, M. Guy, and V. E. Linda. 2003. Reproductive success of bison bulls (*Bison bison bison*) in semi-natural conditions. *Animal Reproduction Science* 79:33–43.
- 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.
- Sauer, P. R. 1984. Physical characteristics. Pages 73–90 in L. K. Halls, editor. *White-tailed deer: ecology and management*. Stackpole Books, Harrisburg, Pennsylvania, USA.
- 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., and W. L. Gannon. 2011. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. *Journal of Mammalogy* 92:235–253.
- Sinervo, B., and C. M. Lively. 1996. The rock-paper-scissors game and the evolution of alternative male strategies. *Nature* 380:240–243.
- Slate, J., T. Marshall, and J. Pemberton. 2000. A retrospective assessment of the accuracy of the paternity inference program Cervus. *Molecular Ecology* 9:801–808.
- 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.
- Stearns, S. C. 1992. *The evolution of life histories*. Volume 249. Oxford University Press, Oxford, United Kingdom.
- Stewart, K. M., R. Bowyer, J. G. Kie, and W. C. Gasaway. 2000. Antler size relative to body mass in moose: tradeoffs associated with reproduction. *Alces* 36:77–83.
- Strickland, B. K., P. D. Jones, S. Demarais, C. M. Dacus, J. R. Dillard, and H. Jacobson. 2013. Estimating Boone and Crockett scores for white-tailed deer from simple antler measurements. *Wildlife Society Bulletin* 37:458–463.
- Turner, M. M., C. S. Deperno, W. Booth, E. L. Vargo, M. C. Conner, and R. A. Lancia. 2016. The mating system of white-tailed deer under Quality Deer Management. *Journal of Wildlife Management* 80:935–940.
- Weir, B. S., and C. C. Cockerham. 1984. Estimating F-statistics for the analysis of population structure. *Evolution* 38:1358–1370.
- Willisch, C., I. Biebach, U. Koller, T. Bucher, N. Marreros, M.-P. Ryser-Dejorgis, L. Keller, and P. Neuhaus. 2012. Male reproductive pattern in a polygynous ungulate with a slow life-history: the role of age, social status and alternative mating tactics. *Evolutionary Ecology* 26:187–206.
- Willisch, C. S., and P. Neuhaus. 2010. Social dominance and conflict reduction in rutting male Alpine ibex, *Capra ibex*. *Behavioral Ecology* 21:372–380.
- Woods, G. R., D. C. Guynn, W. E. Hammitt, and M. E. Patterson. 1996. Determinants of participant satisfaction with quality deer management. *Wildlife Society Bulletin* 24:318–324.

Associate Editor: Christopher Jacques.