



Androgens, antlers, and sexual selection: testosterone's relationship to reproductive success and associated morphological characteristics in white-tailed deer

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Received: 22 April 2022 / Accepted: 1 November 2022 / Published online: 18 November 2022
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Abstract

While hormones such as testosterone are known to drive reproduction and sexually selected traits in many species, research demonstrating a relationship between testosterone and annual or overall reproductive success is sparse. We sought to directly measure how circulating testosterone relates to sexually selected characteristics and reproductive success in a freely breeding population of white-tailed deer (*Odocoileus virginianus*). We captured individuals during September–March annually from 2007 to 2017 and investigated the association between testosterone and antler size, body size, and annual reproductive success for individuals. We also assessed lifetime patterns from individuals captured multiple years. We found a positive relationship between testosterone and body size, and between testosterone and antler size. However, we found a significant interaction between testosterone and age for both body size and antler size response variables, indicating that as age increases, the aforementioned positive relationships with testosterone diminish. Thus, for deer ≥ 6.5 years of age, testosterone is negatively related to body and antler size. In contrast, annual reproductive success, measured by number of offspring sired and recruited into the breeding population, was positively associated with antler size and body size, but not testosterone, age, or an interaction between testosterone and age. Instead, while an individual's average lifetime testosterone had no relationship with overall reproductive success, greater variation in lifetime testosterone was positively related to overall reproductive success. Thus, while we found no significant association between testosterone and annual reproductive success directly, testosterone may be indirectly related to reproductive success through its positive association with antler and body size. Furthermore, understanding how testosterone may fluctuate throughout an individual's lifetime may offer new perspectives in understanding variation in individual reproductive success.

Keywords White-tailed deer · Reproductive success · Sexual selection · Antlers · Testosterone · Androgen

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Introduction

Across the animal kingdom, species display a myriad of characteristics to attract and acquire mates (e.g., antlers, horns, bright colored plumage, etc.). Sexually selected traits play an especially important role in determining fitness of many polygamous species, where the costs of parental care are often limited to one sex (Reynolds and Harvey 1994). While this sex, often female, may increase reproductive success through greater investment in offspring production and rearing, the other sex, often male, may increase their reproductive success through investing in sexually selected traits (Reynolds and Harvey 1994; Wong and Candolin 2005). Variation in sexually selected traits among individuals can come from innate differences in genetic quality (Kruuk et al. 2002; Michel et al. 2016a), differences in immunocompetence (Folstad et al. 1996; Lagesen and Folstad 1998; Hill 2011), and differences in the ability to acquire nutrients (Jones et al. 2018). As a result, these sexually selected traits, while not utilized directly in copulation, often come at a substantial cost and can inform mates of individual quality and condition (Zahavi 1975; Emlen et al. 2012; Warren et al. 2013; Biernaskie et al. 2014), or be used in determining social dominance and competition over access to mates (Clutton-Brock et al. 1979).

In the white-tailed deer (*Odocoileus virginianus*) males may enhance their reproductive success through development of sexually selected traits that communicate overall quality (Zahavi 1975). Antlers, the most outwardly visible sexually selected trait in deer, are argued to be the fastest growing tissue in the animal kingdom (Goss 1968), are grown and shed annually, and come at a high physiological cost (French et al. 1956; Landete-Castillejos et al. 2007; Landete-Castillejos et al. 2012). Consequently, females may use antlers as an indicator of fitness (French et al. 1956; Malo et al. 2009; Michel et al. 2016a) and overall male quality (Ditchkoff et al. 2001a). When females favor a large-antlered, presumably fitter male, they increase the opportunity to improve offspring viability and fitness later in life (Morina et al. 2018). Additionally, antlers play an important role in intrasexual competition. Males may utilize antlers to visually assess potential male competitors and engage in intense physical competitions by locking and clashing antlers. Larger antlers are favored under sexual selection in environments with greater intrasexual competition (Caranza et al. 2020). As a result, antler size plays a role in sexual selection through their use as both ornaments and armaments.

The breeding system of a species consists of the behaviors and mechanisms by which individuals successfully acquire mates and produce offspring. Strategies that males use to increase reproductive success differ depending on the breeding system of a species. For harem-holding species, such as red deer (*Cervus elaphus*) and elk (*Cervus canadensis*; Clutton-Brock et al. 1979, Clutton-Brock et al. 1979), paternity is more likely to be restricted to a small number of dominant, harem-holding individuals. In these species, a male's ability to hold a harem may be affected by characteristics such as antler size and age, but may also be influenced by other external factors such as population density, and environmental stressors may result in greater distribution of paternity among males (Clements et al. 2010). White-tailed deer utilize a tending-bond breeding system, where during a short estrous period (~3 weeks) males pursue females, copulate, and guard them for 24–48 h post-copulation. This tending period helps to ensure that a mate is the sole sire of the litter and may minimize potential breeding from competitors and multiple paternities within a litter (Sorin 2004; Newbolt et al. 2017). However, this system does not allow males to monopolize all females and results in breeding opportunities for males of more varied age and size classes than is found in harem breeding systems, where female congregations

allow a few dominant males to limit competitor breeding opportunities (Sorin 2004; DeYoung et al. 2009; Newbolt et al. 2017). Because of this, population demographics such as population density, age structure, and sex ratio (Newbolt et al. 2017) affect the relative importance of sexually selected characteristics on reproductive success. For white-tailed deer in herds with a high degree of competition among dominant, mature males, factors such as antler size, body size, and age are associated with reproductive success (Lindstedt and Boyce 1985; Forsyth et al. 2005; DeYoung et al. 2006, DeYoung et al. 2009; Ditchkoff 2011; Newbolt et al. 2017; Morina et al. 2018).

Androgens such as testosterone play a dynamic role in all facets of male breeding in mammals. While directly aiding in spermatogenesis and copulation, testosterone also indirectly acts on reproductive efforts. In general, testosterone in deer aids the development of sexually selected traits (Perez-Rodriguez et al. 2006) and increases muscle mass (Griggs et al. 1989, Ditchkoff 2011), social dominance (Chunwang et al. 2004), and signpost communications to potential mates (Miller et al. 1987; Miller et al. 1998). This relationship between testosterone and sexually selected traits is exacerbated in systems with highly competitive social environments, such as populations with greater densities of mature males (de la Peña et al. 2020). Furthermore, increasing testosterone facilitates the final stages of antler development, inducing antler bone matrix synthesis and velvet shedding (Bubenik et al. 1975; Morris and Bubenik 1982; Bubenik et al. 2005); For white-tailed deer specifically, elevated testosterone also increases vocalization frequency, neck swelling, mate chasing, and mate tending (Miller et al. 1987; Pereira et al. 2005; Ditchkoff 2011). During the breeding period, increasing levels of testosterone prepare a male white-tailed deer for the multitude of physiological changes necessary to successfully compete for breeding opportunities.

Most research on reproductive success in cervids and other ungulates has examined how androgen-mediated characteristics like antler size and body size directly affect reproductive success, but research directly relating testosterone to reproductive success is sparse. Research directly measuring this relationship in cervids has been limited to red deer (Malo et al. 2005; de la Peña et al. 2020) and Père David's deer (Chunwang et al. 2004). Testosterone levels themselves may be indicators of reproductive capability, as testosterone is associated positively with sperm concentrations per ejaculate and overall sperm motility and is negatively associated with sperm malformation (Stewart et al. 2018). Additionally, several studies suggest that the composition of bodily excretions such as testosterone metabolites in urine (Miller et al. 1998), glandular secretions used for scent-marking (Quay and Müller-Schwarze 1970; Johnson 1976; Alexy et al. 2003), or darker facial and scrotal pelage (Bubenik and Bubenik 1985) provide potential mates with information regarding testosterone levels. Research assessing the relationship between testosterone concentrations and reproductive success, in addition to the effects of testosterone on sexually selected traits, may provide insight into how testosterone directly influences both annual and lifetime reproductive success.

Just as with other sexually selected traits, the potential drawbacks of maintaining elevated testosterone may prevent individuals in long-lived species from investing in reproductive efforts to the same degree year after year (Bonduriansky et al. 2008; Kokko et al. 1998). This trade-off lends itself to the possibility of different lifetime reproductive strategies, which may offer different degrees of risk and reward. Previous work has found that deer exhibit different lifetime patterns in testosterone, with some individuals more consistent in annual testosterone levels, and others exhibiting greater year-to-year variation (Gomes et al. 2021). Just as different reproductive strategies confer different levels of reproductive success in other species (e.g., bighorn sheep *Ovis*

canadensis, Martin et al. 2013), different lifetime testosterone patterns in white-tailed deer may relate to greater lifetime reproductive output. As long-term individual-level data is rarely collected on long-lived species outside of a completely captive setting, this research presents a unique opportunity to evaluate how reproductive physiology may tie into lifetime reproductive strategies, white-tailed deer life history patterns, and factors influencing lifetime reproductive success.

Building upon previous research, we sought to directly measure how testosterone relates to sexually selected characteristics and annual and overall reproductive success, measured by number of recruited offspring, in a freely breeding population of white-tailed deer. Our study is unique in that we monitored a population of individually marked and annually captured group of captive individuals over a period of ten years. Using these data, we were able to assess how testosterone relates to sexually-selected characteristics known to increase reproductive success, and measure the number of recruited offspring sired by individual males. Furthermore, while lifetime reproductive strategies are often studied at a population-level, such strategies are not often studied at an individual-level (although, for examples, see Hogg 1987; McElligott and Hayden 2000; Festa-Bianchet 2012; and Markussen et al. 2018), making it difficult to detect intraspecific differences in lifetime reproductive strategies. Through long-term monitoring, we could assess how the relationship between testosterone and reproductive success may differ between individuals throughout the course of a lifetime.

Methods study area

We conducted our study at the Auburn Captive Facility; a part of Auburn University's Piedmont Agricultural Research Station, located north of the town of Camp Hill, Alabama. During the time of the study, we maintained a population of 100–120 white-tailed deer within a 174-ha area enclosed by a 2.6-m fence erected in 2007. Deer within the fence consisted of wild deer present in the area and their subsequent offspring. The area experienced no hunting pressure, and no outside deer were introduced into the population during this time. Population numbers were regulated through natural mortality, capture related mortality, and selective release of 6-month-old fawns outside the facility fence (Newbolt et al. 2017).

Within the Auburn Captive Facility, vegetation consisted of 40% agricultural fields and 60% mixed forest. Forested areas had closed canopies with little understory growth. The primary tree species within this area included oak (*Quercus* spp.), hickory (*Carya* spp.), maple (*Acer* spp.), and pine (*Pinus* spp.) of varying age classes. The most prevalent grass species was Bermuda grass (*Cynodon* spp.). However, fescue (*Festuca* spp.), big bluestem (*Andropogon gerardii*), Johnson grass (*Sorghum halepense*), dallisgrass (*Paspalum dilatatum*), and bahia grass (*Paspalum notatum*) were also present. To supplement herd nutrition, we planted multiple agricultural fields with various warm and cool season supplemental forages. The herd also received year-round supplemental nutrition ad libitum from three protein feeders containing 18% protein pellets ("Deer Feed," SouthFresh Feeds; "Record Rack®", Nutrena Feeds). Additionally, four timed-released feeders each deployed approximately 2 kg of shelled corn (*Zea mays*) daily in the fall and winter (Newbolt et al. 2017) to aid in attracting deer for population monitoring and capture purposes.

Field methods

We captured and immobilized deer using a mixture of Telazol® (Fort Dodge Animal Health) and xylazine (Lloyd Laboratories) administered with telemetry darts (2.0 cc, type C, Pneu-Dart Inc.) aimed at the hindquarters. We administered a mixture of Telazol® at a concentration of 125mg/ml and Xylazine at a concentration of 100mg/ml, with each drug given at a rate of approximately 2.2 mg/kg. This mixture was loaded into the darts equipped with radio transmitters and fired using a .22 caliber blank (Kilpatrick et al. 1996). Upon successful sedation, we located deer using VHF telemetry and injected deer with additional tranquilizer mixture if necessary. We then moved deer to an open space appropriate for data collection, collected data, and delivered an intramuscular injection of Tolazoline (1.5 mL/45.36 kg) in equal amounts into the shoulder and hindquarters to reverse immobilization. We then monitored deer at a distance until the individuals demonstrated the ability to move by their own will. All animal handling and research in this study was approved by the Auburn University Institutional Animal Care and Use Committee (PRN 2008–1421; PRN 2010–1785; PRN 2013–2372; PRN 2016–2964; PRN 2019–3599).

Upon initial capture, we aged individuals using tooth replacement and wear (Severinghaus 1949). Although this method may be unreliable at classifying older age classes, it is still reliable for classifying animals younger than 2.5 years of age (Adams and Blanchong 2020). Given that a majority of deer in the study are captured prior to 3 years of age, tooth replacement and wear was assumed to be a reliable means of determining age (Newbolt et al. 2017). Based upon the individual's birth year, we assigned a unique 3-digit individual identification number and visibly displayed this number on ear tags (Severinghaus and Moen 1985; Newbolt et al. 2017). Additionally, we collected a 2-cm² tissue sample from individuals using an ear notch tool and stored at –80 °C in Cryule plastic cryogenic vials (Wheaton, Millville, NJ) to be used later for genetic analyses and determination of parentage. During captures, we also collected 10 ml of blood for testosterone analysis via jugular venipuncture. Blood was then centrifuged at the end of the capture to separate blood cells from serum and stored at –80 °C in Cryule plastic cryogenic vials.

Testosterone measurement

We determined serum testosterone concentrations using enzyme-linked immunosorbent assays (ELISAs). This method has been used to evaluate testosterone concentrations in white-tailed deer (Gionfriddo et al. 2011). Prior to conducting ELISAs, we extracted hormones from serum based off the Steroid Liquid Sample Extraction Protocol from Arbor Assays Inc., with modifications made for available equipment and optimal sample concentrations. We extracted hormones by adding 1 ml ethyl acetate to 0.1 ml serum, vortexing the mixture, then letting the mixture sit for 5 min to allow solvent layers to separate. We then moved samples to a –20 °C freezer, and once the bottom layer of the solution froze, we poured the top solvent layer into another glass test tube. We then repeated this procedure and performed a total of two extractions on samples. We dried extracted samples in a fume hood by submerging glass test tubes in a 60–65 °C water bath in addition to letting the solvent evaporate at room temperature for 12–24 h.

Immediately prior to conducting ELISAs, we dissolved samples at room temperature to a concentration of 0.8 µl using 250 µl DetectX® Testosterone Enzyme Immunoassay Kit

Assay Buffer. Using materials provided in the DetectX[®] Testosterone Enzyme Immunoassay Kit from Arbor Assays Inc., we ran samples through ELISA in duplicates. We read optical density from samples in the completed ELISA plate at 450 nm using Molecular Devices Spectra Max 190 plate reader and Molecular Devices SoftMax[®] Pro (Copyright © 1999–2009 Molecular Devices SoftMax Analytical Technologies, Inc.) software. Using observed optical densities, we calculated testosterone concentrations using MyAssays Ltd. online data analysis tool for the “Arbor Assays Testosterone EIA kit” (<https://www.myassays.com/arbor-assays-testosterone-eia-kit.assay>). Specifically, we compared the absorbances of sample-filled wells to that of standardized samples prepared at known concentrations (10,000 pg/ml, 4,000 pg/ml, 1,600 pg/ml, 640 pg/ml, 256 pg/ml, 102.4 pg/ml, and 40.96 pg/ml). In each assay, we controlled for the possibility of false positives by including wells with no sample or standardized sample, as a negative control. From the absorbance reading of these standardized samples, we created a standardized curve and calculated serum concentrations by comparing serum absorbances to this standardized curve.

Genetic analysis and parentage assignment

We sent tissue samples to DNA Solutions for microsatellite analysis of 18 loci (i.e., Cervid1, L, BM6506, N, INRA011, BM6438, O, BL25, K, Q, D, OarFCB193, P, S, RT5, RT7, RT13, BL42; Anderson et al. 2002, Meredith et al. 2005). Parentage was determined using software Parentage Version 1.1d (Huang et al. 2018). Based upon these data, we compiled a list of candidate parents, and considered an individual to be the parent at the 95% confidence limit. From parentage estimates, we determined annual reproductive success to be the number of offspring recruited into the population (age ≥ 1.5 years) per individual per year, in accordance with previous work done at this facility by Newbolt et al. (2017). Recruitment is a valuable measure of reproductive success and fitness for individuals, as it quantifies the number of offspring that have survived critical mortality periods of early life and are now able to contribute to the effective population (McCullough 1985).

Statistical analysis

To understand the dynamics of testosterone and reproductive success, we examined the relationship among various individual attributes, including testosterone, using program R (v3.6.1; R Core Development Team 2019). Figures were generated using package ggplot2 for program R (Wickham 2016). We used samples collected from September to April for the years 2007–2017 for individuals ≥ 1.5 years old.

Because testosterone concentrations vary with age and temporally during the pre-breeding and breeding seasons (Mirarchi et al. 1978)—our sample period—we standardized testosterone with respect to time of capture and age. To do this, we generated the standardized residual of each individual testosterone concentration compared to the mean testosterone of deer captured in the same month at the same age. In cases where only one individual of an age was captured during a month, expected testosterone level was generated using modeled predictions from other ages and months. Similar methodology is used frequently in the field of psychology (Ayatollahi 1995), and accounts for potential effects of sample month, age, and a month \times age interaction on testosterone that occurs, generating a numeric value that is comparable across our sampling period (Gomes et al. 2021). We refer to this standardized residual as testosterone value.

We assessed the relationship between testosterone value, body size, antler size, and reproductive success using a variety of approaches. To evaluate testosterone's effects on body size, we first generated a single term for body size using the first principal component from a principal component analysis (PCA) that included measurements of chest girth, hind foot length, and body length from tip of the nose to the base of the tail (Newbolt et al. 2017). Henceforth, we refer to the variable generated from this PCA as body size. We used measurements for gross Boone and Crockett antler score (Wright et al. 1997) to assess the relationship between testosterone and antler size. We used linear mixed-effects models to examine the effects of our predictors—testosterone, age, and a testosterone \times age interaction, on response variables of interest, including body size and antler score. We assessed this relationship first treating age as a continuous variable, then using biologically relevant age groupings of 1.5 years, 2.5–3.5 years, 4.5–5.5 years, 6.5+ years. We ran generalized mixed-effects models with a Poisson distribution to assess factors that potentially influence reproductive success. A partial likelihood ratio test indicated that the negative binomial model was not a significant improvement in fit to the data ($P=0.26$), suggesting that there was no substantial overdispersion in our data. First, we modeled the relationship between testosterone, age, and a testosterone \times age interaction on annual reproductive success. A second model on factors influencing annual reproductive success included testosterone, testosterone \times age, body size, and antler size. These variables were included based upon previous literature suggesting their role in reproductive success in white-tailed deer (Newbolt et al. 2017; Morina et al. 2018). In each model, individual ID was included as a random effect to account for heterogeneity in responses among individuals.

To assess how lifetime testosterone patterns relate to overall reproductive success, we subset our data to include only individuals that had been captured at least twice in their life, from the ages of 1.5 and older. Overall reproductive success (ORS) was calculated as the total number of offspring sired over the course of an individual's life. As described in Gomes et al. (2021), we also calculated testosterone range, defined as the range of each individual's testosterone values (maximum – minimum), as well as average testosterone value. We used a generalized linear model to assess if there was a relationship between testosterone range, average testosterone value, and overall reproductive success.

Results

We determined testosterone concentrations for 82 deer over 228 captures from the months of October through March, 2007–2017. Individuals were captured on average 2.45 times, and the greatest number of captures for an individual was 6. Ages of captured individuals ranged from 1.5 years to 12.5 years, and these captures represented over 90% of the adult population (Newbolt et al. 2017). Of these captures, we had 196 captures with complete data collected on testosterone, antler, and body size. These data were used to model the relationship between body size, testosterone, age, and age \times testosterone interaction. Principal component analysis of body measurements generated three components. Principal component 1 explained 95.95% of the variance of the data, and the loadings for chest circumference, body length, and right hind foot length were 0.54, 0.82, and 0.16, respectively (Table 1). Body size was positively associated with both testosterone and age (Table 2; $R^2=0.49$). For each 1 standard deviation increase in testosterone value, standardized for a given month and age, the principal components score for body size increased by 4.12 units (± 3.38 ; 95% C.I.; $P=0.017$). Additionally, for every 1-year increase in age, the principal

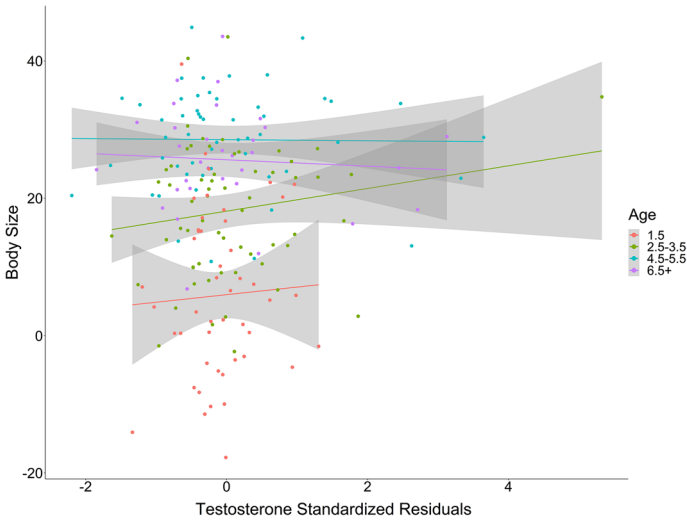


Fig. 1 Testosterone compared to body size (generated from PCA) for male white-tailed deer, grouped by ages of 1.5, 2.5–3.5, 4.5–5.5 and 6.5+. Data came from males captured at the Auburn University Captive Facility, Auburn, AL from September to March, 2007–2017. Testosterone standardized residual refers to testosterone concentrations from these captures, standardized to account for differences in testosterone concentrations due to age or month of capture. 95% confidence intervals and predictions from our top model are shown shaded in grey

Table 1 Summary of principal component analysis (PCA), used to generate a single term for body size in male white-tailed deer. Metrics used to generate a single term for body size included chest circumference, total body length, and right hind foot length. Data shown below reflect the loadings of each metric as they relate to each principal component (Comp. 1, Comp. 2, Comp. 3), eigenvalue, proportion of variance and cumulative variance explained by each principal component. Data were collected from deer captured at the Auburn Captive Facility, September—March 2007—2017

Parameter	Comp. 1	Comp. 2	Comp. 3
<i>Loadings</i>			
Chest circumference	0.54	0.83	
Total body length	0.82	−0.55	0.13
Right hind foot length	0.16		−0.99
Eigenvalue	674.38	22.60	5.89
Proportion of variance	0.96	0.032	0.0084
Cumulative variance	0.96	0.991	1.00

components score for body size increased by 3.68 units (± 0.65 ; 95% C.I.; $P < 0.001$). However, we found a significant interaction between age and testosterone ($P = 0.02$). The negative coefficient estimate for this variable (-0.733 ± 0.307 ; 95% C.I.; $P = 0.02$; Table 2) indicated that with each year increase in age, the positive relationship between testosterone and body size decreased, and by ages > 5.5 , the relationship between testosterone and body size was negative. To better interpret this relationship, we also ran this same model treating age as a categorical variable, using biologically relevant age groupings of 1.5, 2.5–3.5, 4.5–5.5, and 6.5+ (Fig. 1; supplementary material Table S1).

Table 2 Linear mixed effects model results estimating the relationship between skeletal body size (utilizing a single term generated from principal component analysis), and testosterone (T), age as a continuous variable (Age), and a testosterone and age interactive effect (T × Age) in male white-tailed deer captured at the Auburn Captive Facility, September—March 2007—2017

Parameter	Value ± SE	df	T-value	P-value
(Intercept)	3.208 ± 1.587	113	2.021	0.046
T	4.12 ± 1.705	113	2.417	0.017
Age	3.678 ± 0.331	113	11.124	<0.001
T × age	−0.733 ± 0.307	113	−2.389	0.019

We also found a positive relationship between standardized testosterone value and antler size (Table 3; $R^2=0.70$). For each 1 standard deviation increase in testosterone value, antler size increased by 23.9 cm (± 18.75 ; 95% C.I.; $P=0.01$). Furthermore, with every 1-year increase in age, antler size increased by 31.23 cm (± 3.83 ; 95% C.I.; $P<0.001$). However, we also found a significant interaction between age and testosterone in this analysis ($P=0.01$). Again, the negative coefficient estimate (-4.2 ± 1.703 ; 95% C.I.; $P=0.01$; Table 3 indicated that as age increased, the positive relationship between testosterone and antler size decreased. Consequently, by the age of 5.5, we found that the relationship between testosterone and antler score was negative. Again, we further analyzed this relationship by running the same model, but treating age as a categorical variable, with age groupings of 1.5, 2.5–3.5, 4.5–5.5, and 6.5+ (Fig. 2; supplementary material Table S2).

On average, annual reproductive success was 1.08 offspring per male, with a minimum of 0 and maximum of 10 offspring sired by a single individual in a single year. We looked

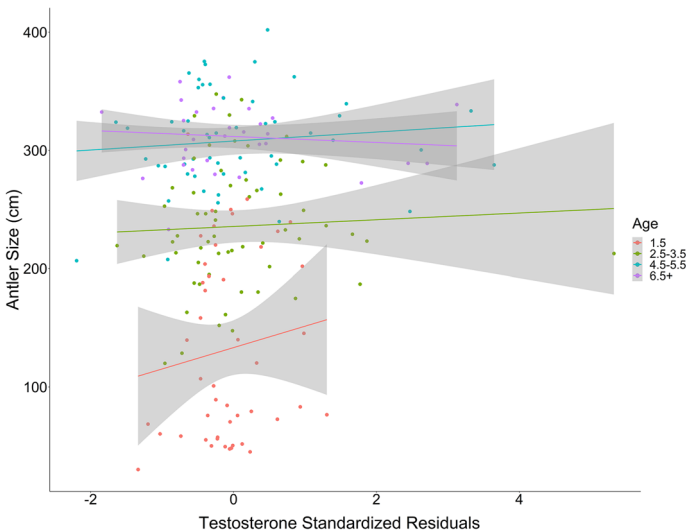


Fig. 2 Testosterone compared to antler score (gross Boone and Crockett score, in cm) for ages 1.5, 2.5–3.5, 4.5–5.5 and 6.5+. Data were obtained from male white-tailed deer captured from the Auburn Captive Facility, Auburn AL, from September—March 2007—2017. Testosterone concentrations were standardized to account for age and month of capture within the sampling period. 95% confidence intervals and predictions from our top model are shown shaded in grey

Table 3 Linear mixed effects model results estimating the relationship between antler size (gross Boone and Crocket score, converted to cm), and testosterone (T), age as a continuous variable (Age), and a testosterone and age interactive effect (T × Age) in male white-tailed deer captured at the Auburn Captive Facility, September—March 2007—2017

Parameter	Value	df	T-value	P-value
(Intercept)	106.798 ± 9.408	113	11.352	<0.001
T	23.880 ± 9.475	113	2.520	0.013
Age	31.226 ± 1.937	113	16.121	<0.001
T × age	-4.190 ± 1.703	113	-2.461	0.019

at models that included quadratic effects of age and, given that these models did not lower the AIC score, opted to use the simpler model without quadratic age effects (Arnold 2010). In a simple model with just age, testosterone, and a testosterone × age interaction, we found that reproductive success showed a significant positive relationship with age (0.17 ± 0.09 ; 95% C.I.; $P = 0.0003$) but a significant negative interaction between testosterone × age (± 0.09 ; 95% C.I.; $P = 0.04$) and reproductive success ($R^2 = 0.55$). Thus, as the level of testosterone increased, the importance of age on reproductive success decreased. Additionally, testosterone alone was positively associated with reproductive success, however these results were not statistically significant (0.44 ; ± 0.50 ; 95% C.I.; $P = 0.07$). These results suggest a potential biologically relevant relationship between testosterone and annual reproductive success, given the marginally insignificant P-value and large effect size (β). However, more data would be needed to understand this relationship more clearly.

In contrast, a full model including all potential factors influencing reproductive success indicated antler score and body size were the only two factors that related to reproductive success (Table 4; $R^2 = 0.70$; Fig. 3). We found a positive association between antler score and reproductive success ($P < 0.001$). For every 25 cm increase in antler score, we saw 1.29 (± 0.14 ; 95% C.I.) times as many offspring sired annually. Thus, compared to animals with the smallest antlers, animals with the largest antlers (a difference of 88.25 cm) would sire 2.48 (± 0.49 ; 95% C.I.) times as many offspring per year. Similarly, we found that body size was positively associated with reproductive success ($P = 0.04$). For every 1-unit increase in principal component score for body size, we found that individuals sired 1.03 times as

Table 4 Generalized linear mixed-effects model results estimating the factors that influence annual reproductive success in male white-tailed deer captured at the Auburn Captive Facility, September—March 2007—2017. Parameters included are antler size (gross Boone and Crocket score, converted to cm), body size (utilizing a single term generated from principal component analysis), testosterone (T), age (Age), and a testosterone and age interactive effect (T × Age). Measures of collinearity among parameters is also reported as variance inflation factors (VIF)

Parameter	Value	Z-value	P-value	VIF
(Intercept)	-4.017 ± 0.602	-6.668	<0.001	
Antler size	0.010 ± 0.003	3.700	<0.001	2.080
Body size	0.029 ± 0.014	2.077	0.038	1.549
T	0.453 ± 0.307	1.479	0.139	1.003
Age	-0.045 ± 0.065	-0.684	0.494	1.434
T × age	-0.092 ± 0.057	-1.595	0.111	

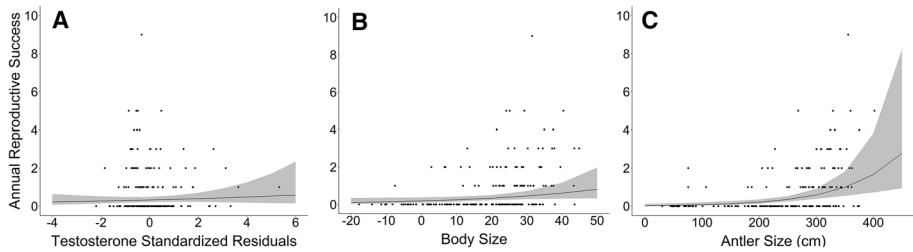


Fig. 3 Factors that relate to annual reproductive success of white-tailed deer. The relationship between testosterone (A), body size (B) and antler size (C) and annual reproductive success of male white-tailed deer. As detailed in Tables 3, the relationship between testosterone and reproductive success was not significant ($P = 0.139$). Both body size ($P = 0.038$) and antler size ($P < 0.001$) were positively associated with reproductive success. Data were obtained from deer captured from the Auburn Captive Facility, Auburn AL, from September—March 2007—2017. Testosterone concentrations were standardized to account for age and month of capture within the sampling period

many offspring per year (± 0.02 ; 95% C.I.). Compared to animals with the smallest body size, animals with the largest body size (a difference of 62.63 principal components) would sire 6.55 (± 1.00 ; 95% C.I.) times as many offspring per year. For each 1 standard deviation increase in scaled testosterone, we observed that a male had 1.57 (± 0.61 ; 95% C.I.) times as many offspring; however, we note that this relationship was not statistically significant ($P = 0.14$). Similarly, we found no relationship between age ($P = 0.49$) or testosterone \times age ($P = 0.11$) and annual reproductive success.

We found that testosterone range was positively related to overall reproductive success ($P = 0.01$). As testosterone range increased by 1 standardized residual, an individual's overall reproductive success increased by 1.28 offspring sired (± 0.97 ; 95% C.I.). We found no significant relationship between overall reproductive success and average testosterone (0.75 ± 1.34 ; 95% C.I.; $P = 0.23$).

Discussion

We found that antler size and body size were the most important predictors of reproductive success in our population of white-tailed deer, whereas we did not find statistical evidence for a direct effect of either testosterone, or age on annual reproductive success. Previous work has shown that females actively select males with larger antlers (Morina et al. 2018), and that antler size is a factor that influences reproductive success in this species (Newbolt et al. 2017), so this finding was unsurprising. Our results were also similar to studies that showed an association between body size and reproductive success (Newbolt et al. 2017). However, although dominance behaviors shown to increase breeding success (DeYoung et al. 2006) often correlate with testosterone concentrations (Lincoln et al. 1972, Miller et al. 1987, Chunwang et al. 2004), in this study our models did not support a statistically significant direct relationship between annual testosterone and annual reproductive success. The aforementioned relationship between testosterone with antler and body size, combined with the positive association between body and antler size with reproductive success, may suggest only an indirect impact of testosterone on reproductive success. These data are supported by the ‘evolutionary potential hypothesis’, where testosterone levels themselves may

not be directly under selection, but downstream effects of testosterone on characteristics such as behavioral traits and sex characteristics are under direct selection (Hau 2007).

Our results are also supported by previous research that has shown that under certain population demographics that support greater intrasexual competition among males, there is likely an increased positive relationship between testosterone and sexually selected traits (de la Peña et al. 2020). The older age structure, balanced sex ratios, and greater deer densities in this study create an environment where male competition and female selectivity for sexually selected traits become more important in gaining reproductive success (Newbolt et al. 2017). Furthermore, while testosterone is positively related to sperm counts and motility, deer are still capable of producing viable sperm during periods of low testosterone (Stewart et al. 2018). Although testosterone facilitates and enhances reproductive efforts, testosterone alone does not guarantee establishment of dominance, survival during the physiologically stressful breeding period, successful mate acquisition and copulation, or offspring recruitment. On the contrary, the direct relationship between antlers and reproductive success seen in our data suggests that factors such as advertising quality through sexually selected traits may be more important in this system.

We instead observed individuals exhibited different patterns in testosterone levels across their lifetime, and that these differences between individuals exhibited a relationship with overall reproductive success. Namely, we found that that increased testosterone range over an individual's lifetime was positively associated with overall reproductive success for deer in our population. Differences in lifetime testosterone patterns may arise from different lifetime reproductive strategies. Intraspecific variation in reproductive strategy has been described previously (e.g. roe deer, *Capreolus capreolus*, Vanpé et al. 2007; white-tailed deer, Lemaître et al. 2018; bighorn sheep, Martin et al. 2013), and is believed to be driven by individual quality (genetics, body size, antler size, dominance, etc.; Zahavi 1975). Our findings suggest that not only do white-tailed deer exhibit different lifetime patterns of hormone secretion, but that these different patterns of testosterone may be ultimately favored under sexual selection and translate to greater overall reproductive success. Because of testosterone's vital role in shaping breeding behaviors, the observed variation of lifetime testosterone patterns in our data suggests that the age and intensity of peak reproductive investment may differ among individuals. While previous research shows that paternity in white-tailed deer may be more widespread among males than originally believed (DeYoung et al. 2002; Sorin 2004; Newbolt et al. 2017), and male white-tailed deer may utilize multiple mating strategies to secure some level of reproductive success, some strategies ultimately result in greater lifetime fitness.

We observed a positive relationship between testosterone and body size for individuals aged 5.5 years and younger. Given previous literature that demonstrates the positive association between testosterone and muscle mass, protein synthesis, and antler growth (Griggs et al. 1989; Killian et al. 2005), this relationship was unsurprising. During this age period, however, individuals allocate resources to somatic growth, during which, testosterone plays a major role. Testosterone facilitates skeletal growth (Young et al. 1989; Phillip et al. 2001), and this is especially important as individuals mature. Similarly, we found a positive relationship between testosterone and age for deer 1.5–5.5 years of age.

Although the relationship between testosterone and antler size in cervids has been cervid debated (Goss 1968, Price and Allen 2004, Bartoš et al. 2009, Demarais and Strickland 2011), as testosterone remains low during the period of antler growth, previous literature generally shows a positive association between testosterone and antler size (Bartoš et al. 2009, Bartoš et al. 2012). One study looking at both captive and wild red deer (*Cervus elaphus*) found a negative relationship between testosterone and antler size, however,

testosterone was positively associated with antler strength (Malo et al. 2009). Additionally, previous research with white-tailed deer has found associations with testosterone and insulin-like growth factor (IGF-I), and IGF-I and antler size (Ditchkoff et al. 2001a). IGF-I promotes testosterone production leading up to the breeding season and is also positively associated with antler growth in multiple cervid species (Schams et al. 1992, Bartoš et al. 2009). It may be through testosterone's relationship with IGF-I that we see the correlation between testosterone and antler size.

Contrary to the patterns we found for deer ≤ 5.5 years of age, deer ≥ 6.5 years had a negative relationship between testosterone and body and antler size. Previous studies with cervids and other large ungulates have documented declines in body mass and muscle mass associated with aging (Yoccoz et al. 2002; Reimers et al. 2005; Nussey et al. 2011). However, since our measure for body size was based upon skeletal measurements, we would not expect a senescent decline in that variable. As a result, our data simply suggest that testosterone is negatively associated with skeletal size in males ≥ 6.5 years, where old individuals that have greater testosterone tend to be those with smaller bodies. While we could find no mention of similar testosterone patterns in the literature, Ditchkoff et al. (2001b) found a similar pattern with respect to antler size and fluctuating asymmetry. They reported that up to age 5.5, there was a negative relationship between antler size and fluctuating asymmetry; however, at 6.5 and older, antler size and asymmetry were positively associated. They suggested that at these older ages, deer may be investing in reproduction so heavily that the associated stress may lead to increased levels of fluctuating asymmetry in antlers. It is possible a similar phenomenon may be occurring in older individuals in our population. Furthermore, older bucks with smaller body size and antler size relative to others within their age classes may need to compensate with increased dominance behaviors to successfully compete for breeding opportunities. These efforts may mitigate a male's inability to invest heavily in somatic growth towards body size earlier in life and inability to allocate significant resources to antler growth during the summer.

It is possible that older males with large antlers and body size have low testosterone because of elevated stress associated with maintenance and development of these tissues (Dmitriew 2011) in combination with behavioral stressors of the breeding season (Bubenik and Leatherland 1984). These stressors could theoretically increase secretion of glucocorticoids, triggering a response along the hypothalamic-pituitary adrenal (HPA) axis and suppressing Leydig cells from producing steroid hormones (Welsh et al. 1982, Cumming et al. 1983). However, we believe it is more likely that larger individuals can obtain breeding opportunities because of their greater antler size (Morina et al. 2018), body size (McElligott et al. 2001), and associated dominance (Chunwang et al. 2004), despite having lower testosterone. These older age classes may represent a point where deer invest in reproduction at a tremendous physiological cost, as senescence is rapidly approaching. These efforts may be the last, and best, opportunity for a male to improve his lifetime fitness prior to senescence (Ditchkoff et al. 2001b). Patterns of hormonal secretion reported in previous studies support this theory. Ditchkoff et al. (2001d) found that IGF-I in male white-tailed deer declined as early as 6.5 years of age, and Bubenik and Schams (1986) reported declines in testosterone after roughly 7 years of age. Reproductive senescence has been described in longer-lived cervids such as red deer (Nussey et al. 2017), with males showing sharp declines in rutting behavior and breeding success, and slight decreases in antler size and number of tines after the age of 9.

Pioneering research in white-tailed deer once stipulated that a few individuals monopolized breeding opportunities within a population (Hirth 1977, McCullough 1979, Marchinton and Hirth 1984, Miller and Ozoga 1997). However, as research techniques advanced,

data showed that reproductive success can be more widely distributed among males in a population, despite large amounts of variation in sexually selected traits such as antlers (Sorin 2004; DeYoung et al. 2006, 2009; Newbolt et al. 2017). Data suggest that while deer of different phenotypes may still achieve some level of reproductive success, greater investment in sexually selected traits, influenced by testosterone level, aid in increasing annual reproductive success. Different lifetime patterns of testosterone, such as a wider range in testosterone values over the course of a lifetime, may represent one lifetime reproductive strategy that also lends itself to the ultimate purpose of sexually selected traits: greater lifetime reproductive output. As this study is one of only a few to document these hormonal patterns in a freely breeding ungulate population, we believe further investigation is warranted. Similar to research with other long-lived ungulates (Martin et al. 2013; Pavitt et al. 2015; Nussey et al. 2017), we believe that research aiming to monitor populations at an individual level while collecting in-depth data on hormonal patterns will aid in efforts to distinguish among reproductive strategies and their potential advantages. As research investigating sexual selection shifts to include genetic and hormonal parameters, evaluating breeding systems and accounting for differences among individuals may provide more insight into the physiological and behavioral dynamics of reproductive strategies in highly competitive breeding systems in long-lived species.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s10682-022-10218-0>.

Acknowledgements We would like to thank the members of the Auburn University Deer Lab for their support during field work, especially, N. Deig, J. Goethlich, N. Ivy-Israel, V. Jackson, C. Moore, S. Rankins, L. Ridgeway, J. Elliott, T. Swartout, and S. Zikeli. Additionally, we are grateful for those who helped fund this research: PRADCO Outdoor Brands, EBSCO Industries Inc., Code Blue Scents, Moultrie Feeders, and support from private individuals.

Author contributions MG: writing—original draft preparation; conceptualization (equal); data curation (supporting); formal analyses (lead); methodology (supporting); project administration (supporting); resources (equal). SD: conceptualization (equal); funding acquisition (lead); methodology (lead); project administration (lead); resources (equal); writing—review and editing. SZ: methodology (supporting); resources (equal); writing—review and editing. WG: writing—review and editing. TS: formal analyses (supporting); writing—review and editing. CN: data curation (lead); funding acquisition (supporting); methodology (supporting); project administration (supporting); resources (equal), writing—review and editing.

Funding This project was financially supported by PRADCO Outdoor Brands, EBSCO Industries. 359 Inc., Code Blue Scents, Moultrie Feeders, and support from private individuals.

Data availability Data can be made available upon request to the authors.

Code availability Not available.

Declarations

Conflict of interest The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Ethical approval All animal handling and research in this study was approved by the Auburn University Institutional Animal Care and Use Committee (PRN 2008 – 1421; PRN 2010 – 1785; PRN 2013–2372; PRN 2016–2964; PRN 2019–3599).

Consent to participate Not available.

Consent for publication Not available.

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