



Phenotypic characteristics of successful parental pairs in white-tailed deer: evidence of non-random mating

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Abstract

Based on principles of natural selection, high-quality individuals may benefit by selecting mates of similar phenotypic quality when given the opportunity; that is, individuals may benefit by engaging in a form of non-random mating referred to as positive assortative mating. In ungulates, the idea of mate selectivity is still highly debated, with few studies providing evidence of positive assortative mating. In white-tailed deer (*Odocoileus virginianus*), recent studies have suggested minimal mate selectivity based on phenotypic characteristics. However, findings from these previous studies may be due to the fact that study populations had young age structures and female skewed sex-ratios that may have limited opportunities for preferential mating. From 2008 to 2019 we studied a captive population of white-tailed deer to examine characteristics of 184 parental pairs that successfully recruited fawns, while the population underwent changes in age structure and sex ratio, and we found evidence of non-random mating in parental pairs. Specifically, for each 1-year increase in male age there was a 0.32-year increase in female age among parental pairs, and for every 1.00 cm increase in male skeletal body size there was a 0.18 cm increase in female skeletal body size. We also observed that as the male and female age structures increased over time, the slope of the relationship between male and female lifetime body percentiles of parental pairs had a greater positive increase over time. Furthermore, we observed that breeding success by younger males decreased as the age structure matured. Although, even with evidence for non-random mating, we were unable to firmly conclude these findings as assortative mating due to the fact we still observed cases where there was a large difference in age between mates, indicating some plasticity with mating. Overall, our results suggest that individuals of an older age and greater body size may select for individuals of a similar condition if provided with the opportunity. However, choosiness appears dynamic, with a decrease in selectivity when preferential mates are limited due to a young age structure or when mating opportunities decrease for poor competitors in a population with a mature age structure.

Keywords Non-random mating · Mating systems · Microsatellites · Recruitment · *Odocoileus virginianus*

Introduction

Prevailing theories on sexual selection in polygynous mammals' state that mating systems are often based on intrasexual competition between males for access to receptive females who may then select for male characteristics that maximize offspring fitness (Darwin 1874; Fisher 1930;

Trivers 1972). Accordingly, it is generally believed that older, socially dominant males with larger bodies, and elaborate ornamentation often have an advantage in intrasexual competition resulting in greater breeding success (Darwin 1871; Emlen and Oring 1977; Clutton-Brock 1989). This is especially true, in ungulates with polygynous mating systems and pronounced sexual dimorphism (Jarman 1983). For decades, researchers generally believed that most, if not all, sexually mature females in a population were bred by a few dominant males (Alexander et al. 1979; Clutton-Brock 1989). However, while female ungulates are expected to limit breeding with low-quality males because of the mother's substantial parental investment (Emlen and Oring 1977; Johnstone et al. 1996), both sexes may select for certain

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attributes or qualities in a potential mate (Dewsbury 1982; Andersson 1994; Jennions and Petrie 1997).

While direct and indirect evidence of female mate choice is becoming more documented in multiple taxa, there remains considerable debate regarding how a female makes mating decisions when basing choice on male intrasexual competition and other possible preferential subtle cues (Andersson and Simmons 2006; Cotton et al. 2006; Clutton-Brock and McAuliffe 2009). Furthermore, there is increasing evidence of male mate choice in the literature (Edward and Chapman 2011), specifically in ungulates (Berger 1989; Preston et al. 2005), further complicating the current understanding of mate selectivity in polygynous species. Prior to recent research, our understanding for decades of mating systems in ungulates was largely based on studies of polygynous species in open landscapes, where breeding behavior was easily observed (Murie 1951; Bergerud 1974; Clutton-Brock et al. 1982; Byers 1997; Wolff 1998). While these studies were greatly informative, they were generally limited to territorial and harem-based mating systems and not necessarily reflective of breeding patterns and mate selectivity in non-territorial systems, such as the tending bond system, which are more common in ungulate species inhabiting more forested landscapes where mating behavior is more difficult to observe. As a result, breeding systems and mate selection strategies for cryptic species such as white-tailed deer (*Odocoileus virginianus*) are poorly understood (Bowyer et al. 2020). For example, Hirth (1977) was only able to observe four confirmed copulations over a two-year span, in what was considered for years to be the seminal work on reproductive patterns of the tending bond system in this species. Even more limiting is the fact that observed breeding events formed a basis of mate selectivity while not accounting for whether or not the offspring of said events were successfully recruited into the adult population.

However, determining parentage using genetic analysis has enabled us to better understand ungulate mating systems (Wilson et al. 2002; Say et al. 2003). In white-tailed deer, reproductive studies using genetic techniques have revealed that monopolization by males is less common than expected: males from multiple age classes successfully breed females (Sorin 2004; DeYoung et al. 2009), and evidence of multiple paternity (two or more sires in litters with more than one offspring) is more common than expected (DeYoung et al. 2002; Sorin 2004; Neuman et al. 2016). These findings are likely due to the fact that a male will often remain with a female for up to 72 h after copulation (DeYoung and Miller 2011), reducing breeding opportunities for that male with other receptive females during that time period. While these studies mentioned previously have provided insight into successful breeding events in white-tailed deer, our understanding of the phenotypic characteristics of parental pairs that

successfully recruit fawns is still poor. Theory postulates that positive assortative mating, a form of nonrandom mating where individuals of closely similar phenotypes choose to mate with each other (Burley 1983; Crespi 1989; Jiang et al. 2013), should occur in populations where variation in the quality of individuals exists, meaning that high-quality individuals should select for mates of a similar quality due to a greater likelihood of offspring survival to adulthood (Fawcett and Johnstone 2003; Cotton et al. 2006). While the broad term ‘quality’ is becoming more saturated in the literature and undergoing scrutiny (Forsythe et al. 2021), age and body size are still commonly used phenotypic characteristics tied to quality, due to them often having a positive relationship with reproductive success (Byers 1997; McEligott et al. 2001; Robinson et al. 2006; Weladji et al. 2006). In white-tailed deer, Neuman et al. (2016) examined age and body size relationships of parental pairs using microsatellite analysis of recruited fawns. They observed no evidence of positive assortative mating and high variability in recruitment success with respect to age and body size relationships in parental pairs, suggesting that random mating was occurring within the population (Neuman et al. 2016). However, the authors believed this may have been due to a young male age structure and female skewed sex ratio that allowed increased breeding opportunity and resulting recruitment success for males of varying sizes and ages (Neuman et al. 2016). These results led us to hypothesize that preferential mating by older individuals of greater body size may occur at a lesser frequency when the probability of finding a mate of similar phenotypic condition is low.

In this study, we examined evidence of successful breeding via fawn recruitment in a captive population of white-tailed deer allowed to breed naturally. Our primary objective was to improve understanding of the age and body size of parental pairs that successfully recruited fawns. This study utilized the same population and expanded on the dataset used by Neuman et al. (2016). Because the overall age structure had increased, and the sex-ratio had become more balanced since that study, we also had the objective to determine whether age and body size characteristics of parental pairs were influenced by the age structure, density, and sex ratio of the population over time. Furthermore, we divided parental pairings into categorical age-classes with the objective of examining the proportion of each grouping successful in fawn recruitment in relation to the demographic effects mentioned in the previous sentence (i.e., age structure, density, and sex-ratio). Finally, we also examined the characteristics of parental pairs involved in multiple paternity events to better understand this unique phenomenon. We hypothesized we would find evidence of non-random mating, based on age and body size, occurring within the population. Following this, we also hypothesized we

would observe positive assortative mating based on age and body size in parental pairs due to an increased selection of potential mates of older age classes with greater body size due to a maturing age structure and sex ratio near parity in the population. Finally, we also hypothesized that multiple paternity events would reveal age and body size differences between sires, indicating the theory of male displacement as a possible explanation of multiple paternity in white-tailed deer (Sorin 2004).

Materials and methods

Study area

This study examined a captive population of white-tailed deer at the Auburn Captive Facility (ACF) in Camp Hill, Alabama. The facility was created in 2007 and was 174 ha surrounded by a 2.6 m fence. The population consisted of individuals and descendants of individuals who inhabited the area when the fence was installed in 2007. The population received no hunting pressure and fawn predation was not documented, but coyotes (*Canis latrans*) and bobcat (*Lynx rufus*) were occasionally observed within the facility.

The facility was undeveloped with no building structures or roadways within. The land cover types within the facility consisted of open fields (44%) and mixed forests (56%; Swartout et al. 2023b). The primary tree species within ACF included oak (*Quercus* spp.), sweetgum (*Liquidambar styraciflua*), hickory (*Carya* spp.), and loblolly pine, (*Pinus taeda*) with an understory of blackberry (*Rubus* spp.), eastern red cedar (*Juniperus virginiana*), and Chinese privet (*Ligustrum sinense*). Prescribed fire was applied on occasion throughout forested portions of the property. The predominant grass species within ACF was Bermuda grass (*Cynodon dactylon*), but fescue (*Festuca* sp.), big bluestem (*Andropogon gerardi*), Johnson grass (*Sorghum halepense*), dallisgrass (*Paspalum dilatatum*), and bahia grass (*P. notatum*) were also present. Elevation ranged from 190 to 225 m above sea level and several creeks flowed through ACF and served as a source of water. The climate of Camp Hill, Alabama was classified as humid subtropical with a temperature throughout the year ranging from an average low of -0.5 °C in January to an average high of 32.5 °C in August, with an average annual precipitation of 137 cm based on data from the nearest weather station (NOAA National Centers for Environmental information 2022). Herd nutrition was supplemented with food plots planted in warm and cool season forage and protein feeders. Protein was available ad libitum all year at feeders containing pellets that were 18% protein (Record Rack[®], Nutrena Feeds; Minneapolis, MN). For attracting deer for capture purposes, whole corn (*Zea*

mays) was provided in the fall and winter at feeders (Newbolt et al. 2017).

Capture techniques

Deer were captured mid-September to mid-March annually from 2008 to 2019 using two techniques. From 2008 to 2013, deer were captured using a capture facility or cartridge-fired dart guns. The capture facility was 0.8 ha and allowed for capture of multiple individuals at one time and is further described by Neuman et al. (2016). Beginning in 2014, all deer were immobilized and captured by darting. Dart guns were fitted with night vision scopes and fired telemetry darts using 0.22 caliber blanks (Kilpatrick et al. 1996). The telemetry darts (2.0 cc, type C, Pneu-Dart Inc., Williamsport, PA) held a mixture of Telazol[®] (at a concentration of 125 mg/ml and given at a rate of 2.2 mg/kg) and Xylazine (at a concentration of 100 mg/ml given at a rate of 2.2 mg/kg) (Kilpatrick et al. 1996). To ensure minimal chance of capture-related mortality and given our research objectives were to examine parental pairs that successfully recruited fawns, deer were not darted until at least 6 months of age. Darters sat in elevated tree stands overlooking feeders and shot deer in the hindquarter muscle mass to ensure a safe and effective intramuscular injection of the sedatives (Kilpatrick et al. 1996; Miller et al. 2003). Tracking of immobilized deer was done with VHF radiotelemetry with a receiver and 3-element Yagi antenna (Kilpatrick et al. 1996). Tolazoline (1.5 mL/45.36 kg) was administered intramuscularly in the front shoulder and hindquarter muscle masses to reverse sedation at completion of handling procedures (Miller et al. 2004).

Data collection

All deer were aged using the tooth replacement and wear technique (Severinghaus 1949) and given a unique six-digit identification number. We considered a deer known age if it was determined to be ≤ 1.5 years old at time of capture, due to the high accuracy of the technique with these age classes (Gee et al. 2002). Following the methods of Neuman et al. (2016), three skeletal body size measurements were taken using a flexible measuring tape and listed as the following: body length (tip of the snout to the proximal end of the tail, following a straight line along the backbone), hind foot length (measured from the tip of the hoof to the posterior end of the tuber calcis), and chest girth (circumference of the chest directly posterior of front legs). We attempted to capture individuals multiple times in their lifetime to get up-to-date information and accurate estimates of skeletal body size. We obtained a tissue sample from the ear for genetic analysis using a notching tool to remove a 1-cm² piece of

tissue. For preservation, samples were placed in Cryule plastic cryogenic vials (Wheaton, Millville, NJ) and then placed in a $-80\text{ }^{\circ}\text{C}$ freezer as recommended by Shabihkhani et al. (2014). All animal handling and research in this study was approved by the Auburn University Institutional Animal Care and Use Committee (PRN 2008–1417; PRN 2008–1421; PRN 2010–1785; PRN 2011–1971; PRN 2013–2372; PRN 2014–2521; PRN 2016–2964; PRN 2016–2985; PRN 2019–3599; PRN 2019–3623) and were in compliance with guidelines adopted by the American Society of Mammalogists Animal Care and Use Committee (Sikes et al. 2016).

Microsatellite analysis and parentage assignment

All tissues samples were sent to DNA Solutions (Oklahoma City, OK) for microsatellite marker analysis of 18 loci (e.g., Cervid1, BM6506, BM6438, INRA011, OarFCB193, N, Q, D, K, O; Anderson et al. 2002). We used the software program Parentage 1.1d (Huang 2018) to determine allelic composition, gene diversity (Nei 1987), and allelic richness (El Mousadik and Petit 1996). Significant departures from the Hardy-Weinberg equilibrium were observed at 2 of the 18 loci (Supplementary Table S1); however, these loci were still included in our parentage assignment analysis due to the software Parentage 1.1d accounting for null alleles and inbreeding (Dakin and Avise 2004; Huang et al. 2018).

From 2008 to 2019 we created an annual list of candidate parents for ACF. All individuals ≥ 6 months of age were listed as a candidate parent; fawns were included in a year's list of candidate parents due to prior studies finding evidence of male and female fawns breeding (Nixon 1971; Rhodes et al. 1986; Schultz and Johnson 1992; Karns et al. 2014; Neuman et al. 2016). An individual was listed as a candidate parent annually if it was detected through camera surveys, or by visual observation by researchers while at the facility. If an individual was not detected for two consecutive years through these methods, it was determined to be deceased and not included in any further candidate parent lists.

We determined parentage of each annual cohort of recruited fawns using the likelihood-ratio method in a parent-pair analysis in Parentage 1.1d (Jones and Arden 2003; Huang et al. 2018). Parentage 1.1d determined confidence levels using critical levels of the delta statistic after conducting simulations (i.e., 10,000 iterations) with our lists of annual candidate fathers and mothers, a loci mistype error rate of 0.01, an inbreeding coefficient (Weir and Cockerham 1984) of 0.074 (as determined by prior research, Newbolt et al. 2017; Huang et al. 2018), and an assumption that 90% of the population in ACF was genetically sampled. Parentage was only assigned to individuals initially captured at ≤ 1.5 years of age (known-aged individuals) to ensure with high probability that an individual was aged correctly using the

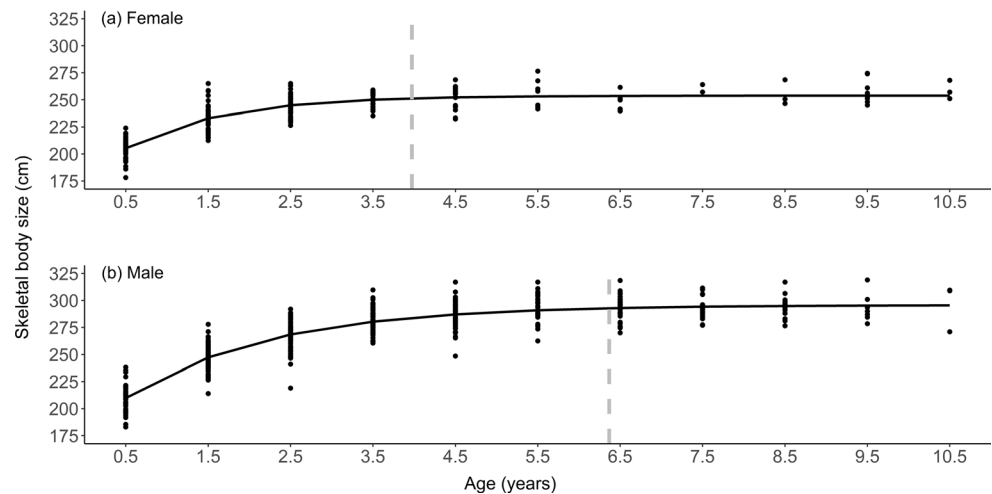
tooth replacement and wear technique (Gee et al. 2002). We only confirmed parentage if at minimum the trio pair (greatest likely paternity and maternity assignment) confidence level was 95%, similar to methods used in prior studies at ACF (Neuman et al. 2016; Newbolt et al. 2017; Ivy-Israel et al. 2020; Gomes et al. 2023; Swartout et al. 2023a).

Statistical analysis

We used three skeletal measurements (hind foot, body length, and chest girth) to represent body size and skeletal growth (Smart et al. 1973; Roseberry and Klimstra 1975; Bartareau 2019). To create one numeric value for skeletal body size, we added all three measurements together to create a total measurement in centimeters for the given year the measurements were taken (hereafter called body size), similar to prior studies at ACF (Neuman et al. 2016; Newbolt et al. 2017; Swartout et al. 2023a). Due to our inability to obtain measurements every year of an individual's life, we created lifetime body size values that could be used in our analyses. First, we examined skeletal body growth curves of each sex to determine when asymptotic growth was achieved (e.g., cessation of skeletal growth). We used a von Bertalanffy growth curve (von Bertalanffy 1938) to determine for each sex at what age 99% of asymptotic skeletal size was achieved. We determined that 99% of skeletal size was reached at 3.97 years of age in females and 6.37 years of age in males (Fig. 1), similar to Ditchkoff et al. (1997) and Ditchkoff (2011). Based on these findings, we set maximized skeletal growth at 4.5 years of age in females and 6.5 years of age in males. Measurements collected at or after physical maturity in both sexes were determined to be mature skeletal measurements (hereafter termed maximized body measurement). If an individual was determined to have successfully mated after reaching this point, and it had at least one maximized body size measurement collected, we used that measurement for the year it was known to have successfully mated. For example, if it was determined a female was bred at 8.5 years of age but a measurement had not been obtained since 5.5 years of age, we used the body size measurement taken at 5.5 years of age in our analysis since maximized skeletal growth occurs in females by 4.5 years.

Like Neuman et al. (2016), we also calculated a lifetime body percentile (LBP) and used this statistic as a surrogate for skeletal body size. Specifically, we pooled body size measurements across all years to determine an individual's size placement within each age group (e.g., an individual in the 25th percentile out of 65 individuals at 2.5 years of age). That percentile could then be utilized as a body score for that individual the year it was collected, assuming that individual had documented reproductive success. Furthermore,

Fig. 1 von Bertalanffy growth curves of (a) female and (b) male white-tailed deer at the Auburn Captive Facility, Camp Hill, Alabama, from 2008 to 2019. Dashed gray lines represent the point in age where 99% of maximized skeletal growth was achieved



if an individual had at least two body percentiles calculated at different ages during its lifetime we calculated the average and used this mean as the individual's lifetime body percentile. The lifetime body percentile could then be used as a body size score for years where an individual successfully mated but no measurements were collected. Thus, to test our hypothesis of assortative mating of parental pairs based on body size we used three separate datasets in our analyses: a dataset where body size measurements were collected within a year of the breeding event ($n = 24$ pairings), a dataset where individuals had body size measurements collected within the last year and including any maximized body size measurements ($n = 81$ pairings), and a dataset where both individuals had a lifetime body percentile ($n = 110$ pairings). For analysis, in the software program R (version 4.3.1; R Core Team 2023) we used linear mixed-effects models with male body size or male LBP as the predictor variable in relation to the response variable of female body size or female LBP, with individual as a random effect. To test our hypothesis for possible demographic effects on body size relationships, we conducted additional models where we included variables for annual average male age structure (AMA), annual average female age structure (AFA), year (Year), annual density (Dens), and annual sex ratio (SR) while also including an interaction term for each of these variables in relation to body size. We examined each demographic variable in a separate analysis due to detection of collinearity among predictor variables in the full model based on variance inflation factors (SR: 3.37, AMA: 60.49, AFA: 18.57, Year: 97.77, Dens: 3.17) using the car package (Fox et al. 2012) in the program R.

To test our hypothesis of non-random mating of parental pairs based on age, we first conducted a chi-squared test where we compared the groupings of observed differences in age (e.g., 2 years, 5 years) between the sire and dam in parental pairs to the expected age difference between

parental pairs assuming random mating within the population. Expected age differences were based on our annual candidate parent lists where we examined all possible annual combinations from 2008 to 2019 in ACF. For our chi-squared test, we deemed repeated measures to not be of concern due to the low frequency of observed parental pairs that bred together more than once during the study period. Next, we examined age relationships between parental pairs in the program R using a linear mixed-effects model with male age as the predictor variable in relation to the response variable of female age with individual as a random effect. To test our hypothesis that demographic effects may influence age-based assortative mating, we once again included demographic variables (AMA, AFA, Year, Dens, SR) in our age analysis and an interaction term was included for each respective variable. Collinearity was detected between predictor variables in the full model based on variance inflation factors (SR: 6.16, AMA: 77.65, AFA: 17.95, Year: 118.21, Dens: 5.85), and as a result, each demographic variable was examined in a separate analysis. Additionally, to test for demographic effects on age-based assortative mating, we divided parental pairs into three categories: "Both Young Adults", "One Young Adult", and "Two Mature Adults", we then used linear regression to examine the annual percentage of each grouping observed successfully recruiting fawns over time within the population. We categorized these groups based on our previous findings for maximized skeletal size, we considered mature adults to be any female ≥ 4.5 years of age and any male ≥ 6.5 years of age. To test our hypothesis of multiple paternity, we used a Mann-Whitney U test to compare age and skeletal body size characteristics of mates of multiple paternity events to non-multiple paternity events. We used a Mann-Whitney U test due to indications the data violated the assumption of normality. Furthermore, when examining the annual number of occurrences of multiple paternity events, we used a Fisher's exact

Fig. 2 Number of individual white-tailed deer of each respective age grouping (colored bars) for females (a) and males (b) at the Auburn Captive Facility, Camp Hill, Alabama, from 2008 to 2019. The number above each bar grouping represents the average age of all individuals of that respective sex within the herd that year. Data were based on candidate mother and father lists (including fawns)

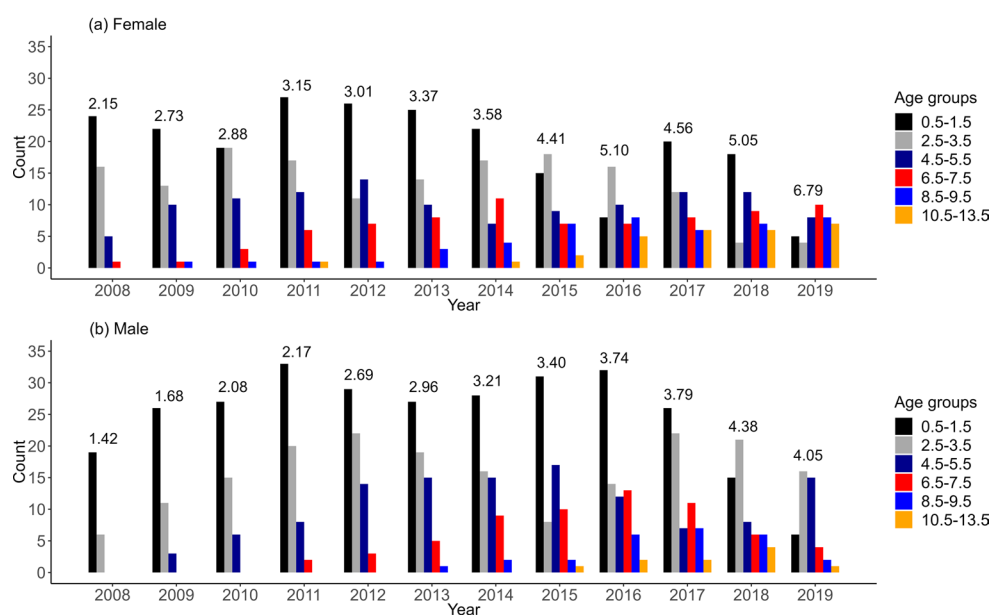
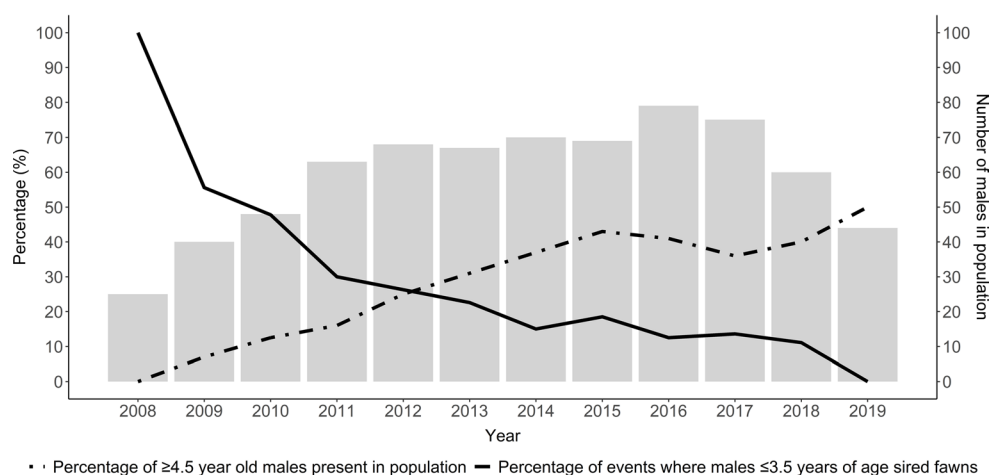


Fig. 3 Left Y-axis: Percentage of male white-tailed deer ≤ 3.5 years of age that sired a recruited fawn (black solid line) and the percentage of males ≥ 4.5 years of age present in the population (black dashed line) at the Auburn Captive Facility, Camp Hill, Alabama, from 2008 to 2019. Right Y-axis: Number of male deer (gray bars) within the population each year



test to test for a significant association between type of litter event (multiple paternity or non-multiple paternity) and segment of the study (2008 to 2013 or 2014 to 2019) to account for a changing age structure. All figures were created using the package ggplot2 (Wickham 2016) in the program R. Finally, all body size and age models mentioned previously were tested to ensure that model assumptions were met prior to analysis.

Results

Annual camera surveys and capture and mortality records indicated that the population of ACF ranged annually from 71 to 139 individuals during 2008–2019 (Supplementary Table S2). Population density generally increased from the beginning of the study until 2017, and the adult sex ratio was female skewed until 2011, when it became slightly

male skewed for the rest of the study period. The female age structure matured during the study: average age of candidate dams (including female fawns) in 2008 was 2.15 years ($SE=0.24$, $n=46$) and peaked in 2019 at 6.79 years ($SE=0.53$, $n=42$; Fig. 2a). Similarly, the male age structure matured from 1.42 years ($SE=0.20$, $n=25$) in 2008 to a peak of 4.38 years ($SE=0.40$, $n=60$; Fig. 2b) in 2018. The percentage of recruitment events where a male ≤ 3.5 years of age sired a fawn decreased over time as the percentage of males ≥ 4.5 years of age increased in the population (Fig. 3), with no documentation in 2019 of any of the 22 known males ≤ 3.5 years of age siring a fawn (Supplementary Fig. S1). Specifically, a linear regression between these variables found that for every 1% increase in males ≥ 4.5 years of age present in the population, known sires that were ≤ 3.5 years of age decreased by 1.55% ($95\% C.I. = 1.05–2.05$, $t_{10} = -6.94$, $P < 0.001$). We recorded 383 recruited fawns during the study, 309 of which were known age. We

Fig. 4 Observed age differences (black bars) of parental pairs of white-tailed deer compared to expected age differences assuming random mating (gray bars) at the Auburn Captive Facility, Camp Hill, Alabama, from 2008 to 2019. Negative values represent when the sire (male) was older than the dam (female) and positive values represent when the dam was older than the sire

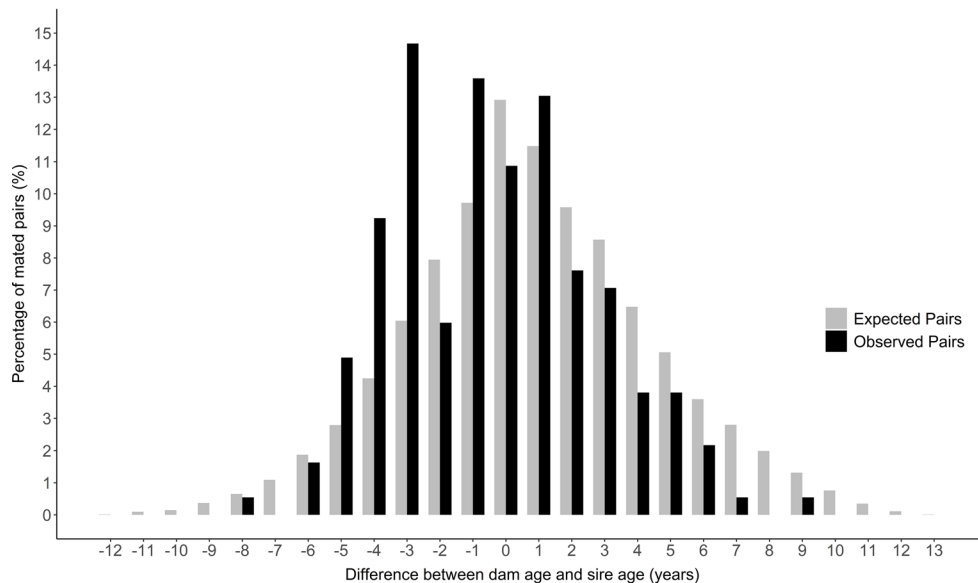
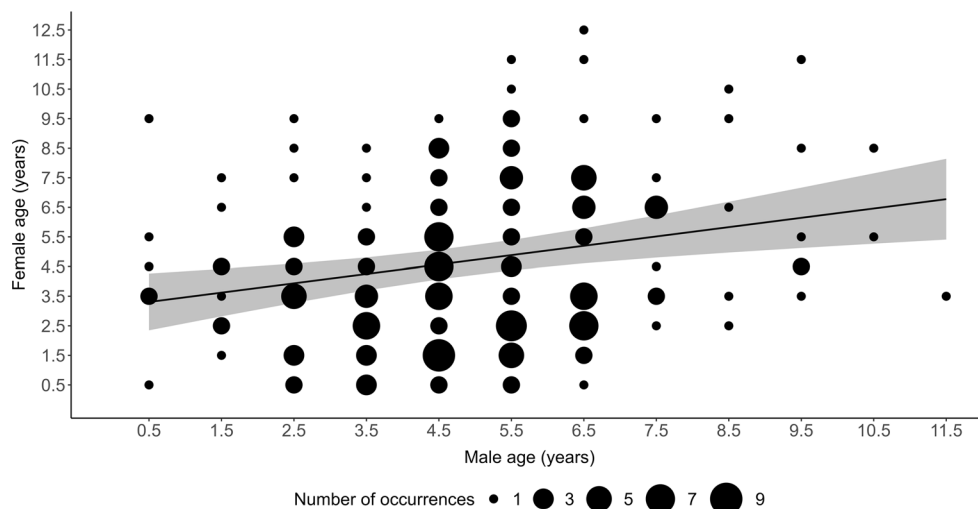


Fig. 5 Age relationships of 184 parental pairs of white-tailed deer at the Auburn Captive Facility, Camp Hill, Alabama, from 2008 to 2019. Size of dots represents the number of occurrences of pairings at that specific sire and dam age while the black line represents the regression line of the linear mixed-effects model ($\beta=0.32$; $P=0.002$) and its respective 95% confidence intervals (shaded gray area)



were able to identify both parents at the 95% confidence level for 211 of these fawns that came from 184 litters. Of the 184 pairings, only 6 pairings (3.26%) involved a dam and sire breeding more than once during the study period. Interestingly, 4 of these 6 pairings involved a dam and sire breeding in consecutive seasons.

The overall distribution of age differences between parental pairs was significantly different than the expected distribution of age differences from a random assortment of mates ($\chi^2_{25}=59.36$, $P<0.001$; Fig. 4). We found that cases where the male was 3 to 4 years older than the female had the greatest difference in observed versus expected frequency. The greatest observed age difference between mates was 9 years, where a 9.5-year-old female bred with a male fawn. In separate events, the oldest female and male to successfully breed were 12.5 and 11.5 years of age, respectively. We observed 16 parental pairs where at least one of the parents

was a fawn, and one case where two fawns were observed to have successfully bred and recruited offspring. When examining age between males and females for 184 parental pairs using a linear mixed-effects model, we found a significant relationship where for every 1-year increase in male age we saw a 0.32-year increase in female age (95% C.I. = 0.12–0.51, $t_{128}=3.25$, $P=0.002$; Fig. 5). However, we found that the relationship between male and female age was no longer significant when including the demographic variables AMA ($P=0.907$), AFA ($P=0.839$), Year ($P=0.998$), or SR ($P=0.056$) within the model but remained significant when including Dens ($P=0.002$). When examining models with interaction terms, we did not detect a significant interaction between our predictor variable for individual age and AMA ($P=0.077$), AFA ($P=0.613$), Year ($P=0.154$), Dens ($P=0.233$), or SR ($P=0.124$). When dividing parental pairs into three categorical age groupings (i.e., both mature,

Fig. 6 Annual percentage of parental pairs of white-tailed deer at the Auburn Captive Facility, Camp Hill, Alabama, from 2008 to 2019. Groupings included: where both individuals were young adults (black dashed line), one individual was a young adult (black solid line), or both individuals were mature adults (solid gray line). Males ≥ 6.5 and females ≥ 4.5 years of age were considered mature adults based on determination of cessation in skeletal growth

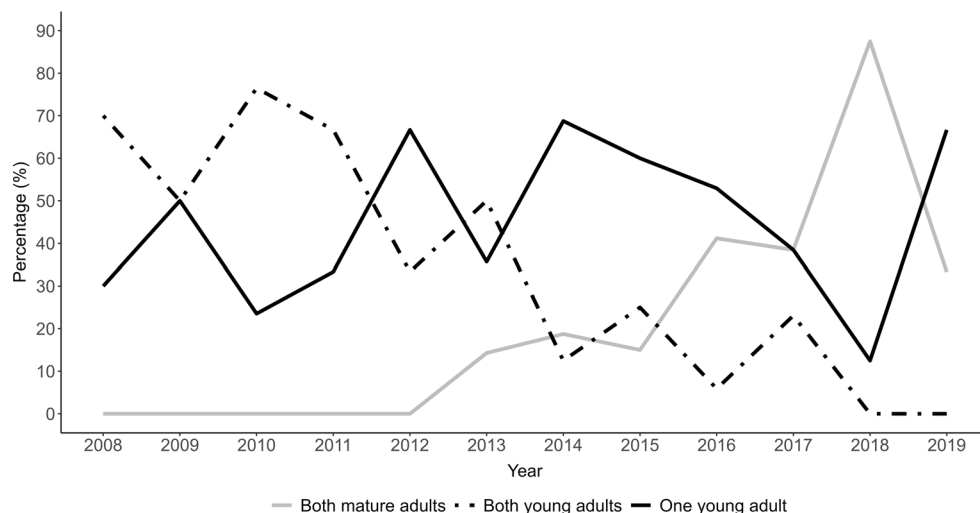
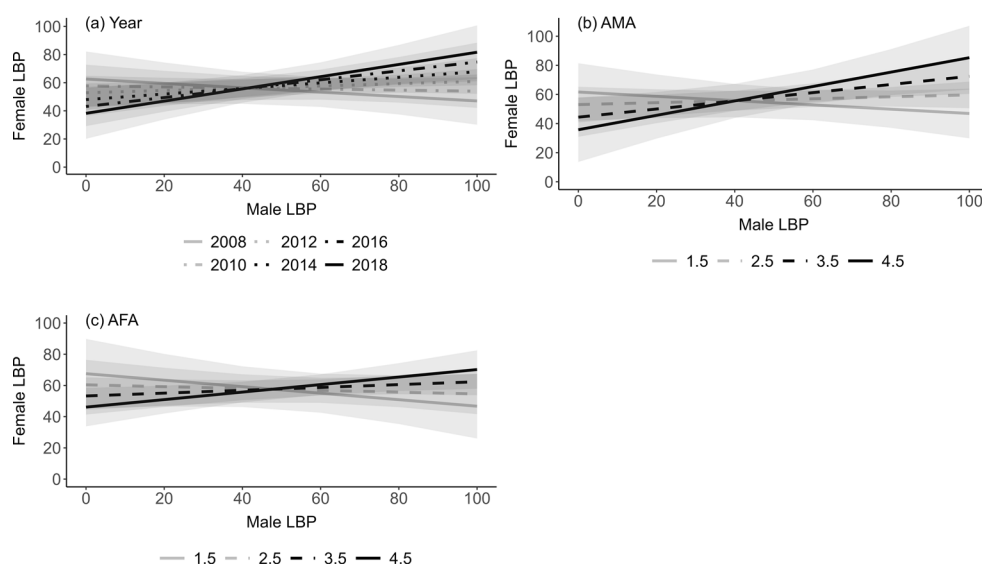


Fig. 7 The relationship between lifetime body percentiles (LBP) of parental pairs in relation to different (a) years, (b) average annual male age structure (AMA), and (c) average annual female age structure (AFA) of white-tailed deer at the Auburn Captive Facility, Camp Hill, Alabama, from 2008 to 2019. Shaded gray areas represent 95% confidence intervals for each respective regression line



one young, and both young), we observed that as the age structure matured for both sexes, the percentage of mature parental pairs increased, and younger pairings decreased. Specifically, using linear regression we found for every 1-year progression in the study the percentage of mature parental pairs increased by 5.87% (95% C.I. = 2.84–8.90, $t_{10}=4.31$, $P=0.002$; Fig. 6), while pairings where both adults were young decreased by 6.85% (95% C.I. = 4.41–9.30, $t_{10} = -6.24$, $P < 0.001$), we detected no significant relationship when only one of the individuals of the pair was young ($t_{10}=0.613$, $P=0.554$). Furthermore, as the average male age structure increased by 1-year, pairings where both adults were young decreased by 25.86% (95% C.I. = 17.04–34.68, $t_{10} = -6.53$, $P < 0.001$), and decreased by 17.56% for every 1-year increase in the average female age structure (95% C.I. = 9.33–25.80, $t_{10} = -4.75$, $P < 0.001$). Also of note, the percentage of successful parental pairs that involved at least one parent ≤ 1.5 years of age decreased by

5.25% for every 1-year progression in the study (95% C.I. = 2.50–8.03, $t_{10} = -4.25$, $P=0.002$).

Using a linear mixed-effects model, we observed no significant relationship between lifetime body percentiles of 110 parental pairs ($t_{66}=1.36$, $P=0.180$). Furthermore, we found that the relationship between male and female lifetime body percentiles remained non-significant when including the demographic variables AMA ($P=0.167$), AFA ($P=0.205$), Year ($P=0.168$), SR ($P=0.154$), and Dens ($P=0.232$) in each of their own respective models. However, when examining these models with interaction terms, we found significant interactions between our predictor variable for individual LBP and AMA ($P=0.036$), AFA ($P=0.043$), and Year ($P=0.028$), but not Dens ($P=0.259$) or SR ($P=0.184$). We found that as the male and female age structures increased over time, the slope between male and female LBP increased (Fig. 7). Similarly, for each 1-year

increase in the study, the slope between male and female LBP increased.

Using skeletal body size measurements, we had 81 confirmed parental pairs where we accepted measurements within the last year, or the animal was mature and had a maximized body measurement. Using a linear mixed-effects model, we found a significant relationship where female skeletal body size increased by 0.18 cm for every 1.00 cm increase in male skeletal body size (95% C.I. = 0.03–0.34, $t_{42}=2.34$, $P=0.024$; Fig. 8). Furthermore, we found that the relationship between male and female skeletal body size remained significant when including the demographic variables AMA ($P=0.015$), AFA ($P=0.006$), Year ($P=0.011$), SR ($P=0.025$), and Dens ($P=0.041$) in each of their own respective models. However, when examining these models with interaction terms, we did not detect a significant interaction between our predictor variable for individual skeletal body size and AMA ($P=0.495$), AFA ($P=0.429$), Year ($P=0.415$), Dens ($P=0.756$), or SR ($P=0.836$). While statistically not significant, a graphical examination of these models revealed similarities to what was observed when examining the relationship between LBP of parental pairs and the interactions with AMA, AFA, and Year (Supplementary Fig. S2). When examining parental pairs where we only included body measurements that were collected the year of, we had 24 pairings. Using a linear mixed-effects model, we observed no significant relationship between body size of parental pairs ($t_4 = -0.10$, $P=0.923$). Furthermore, we found that the relationship between male and female skeletal body size remained non-significant when including the demographic variables AMA ($P=0.983$), AFA ($P=0.906$), Year ($P=0.971$), SR ($P=0.994$), and Dens ($P=0.768$) in each of their own respective models. When examining these

models with interaction terms, we did not detect a significant interaction between our predictor variable for individual skeletal body size and AMA ($P=0.573$), AFA ($P=0.812$), Year ($P=0.618$), Dens ($P=0.232$), or SR ($P=0.268$).

Of 38 litters with > 1 fawn, we observed 12 cases of multiple paternity where the trio confidence level was at least 95%, and 6 additional cases where the trio confidence didn't meet our minimum threshold; these 6 additional cases were excluded from further analysis. Out of 12 multiple paternity events, 10 (83.3%) occurred in 2013 or before (Supplementary Fig. S3). However, using a Fisher's exact test we found no statistical significance ($P=0.158$) between the number of multiple paternity events and whether it was early or late in the study. The average age of females in non-multiple paternity events (litter > 1 with one sire) was 4.69 years ($SE=0.35$, $n=26$), but was 5.58 years ($SE=0.72$, $n=12$) in cases of multiple paternity; using a Mann-Whitney U test we found no significant difference in age between groups ($W=113.5$, $P=0.181$). When a male was the sole sire of a litter, the average age of the male was 5.73 years ($SE=0.43$, $n=26$), but was 4.46 years ($SE=0.44$, $n=24$) in cases of multiple paternity; using a Mann-Whitney U test we found no significant difference in age between groups ($W=404.5$, $P=0.068$). The average age difference between a female and male during a non-multiple paternity event was 1.96 years ($SE=0.39$, $n=26$), and was 2.21 years ($SE=0.34$, $n=24$) during a multiple paternity event, using a Mann-Whitney U test we found no significant difference in the age difference of parental pairs between groups ($W=356.5$, $P=0.38$). In 9 of the 12 cases of multiple paternity the female was older than at least one of the males in the event. The average age difference between males during multiple paternity events was 1.92 years ($SE=1.68$, $n=12$). Interestingly, all 4 cases

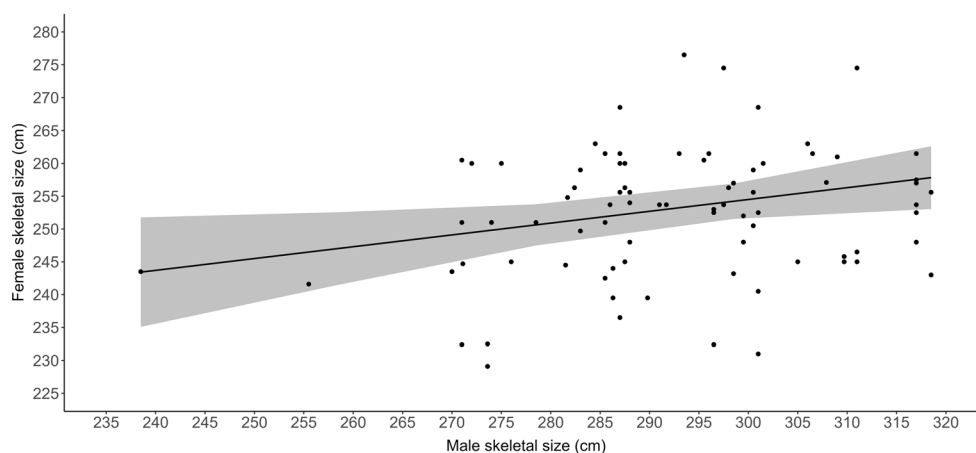


Fig. 8 The relationship between skeletal body size of 81 parental pairs of white-tailed deer at the Auburn Captive Facility, Camp Hill, Alabama, from 2008 to 2019. The body measurement used was either one that was collected within a year of the breeding event ($n=46$), or a mature body measurement collected for a mature individual earlier in

the study ($n=35$). Points represent the raw data and the black line represents the regression line of the linear mixed-effects model ($\beta=0.18$; $P=0.024$) and its respective 95% confidence intervals (shaded gray area)

of multiple paternity that occurred in 2013 or later involved males that were ≥ 4.5 years of age. Examining skeletal body size, the average body size of females during multiple paternity events was 249.5 cm ($SE=3.6$, $n=10$), and 253.2 cm ($SE=1.9$, $n=24$) during non-multiple paternity events (litter > 1 with one sire); using a Mann-Whitney U test we found no significant difference in body size between groups ($W=125.5$, $P=0.85$). The average size of males during multiple paternity events was 293.8 cm ($SE=2.6$, $n=14$), and 289.1 cm ($SE=3.6$, $n=21$) for a male during non-multiple paternity events; using a Mann-Whitney U test we found no significant difference in body size between groups ($W=125.5$, $P=0.479$). The average skeletal body size difference between a female and males during a multiple paternity event was 39.0 cm ($SE=11.8$, $n=11$), and 37.9 cm ($SE=3.8$, $n=17$) between a female and male of a non-multiple paternity event; using a Mann-Whitney U test we found no significant difference in the body size difference of parental pairs between groups ($W=99.5$, $P=0.796$). The average skeletal body size difference between males of multiple paternity events was 13.40 cm ($SE=4.68$, $n=5$).

Discussion

In support of our overall hypothesis, we found evidence of non-random mating, based on age, occurring within the population. However, we also observed plasticity in the age differences of mated pairs that do not fully support evidence of assortative mating. Furthermore, we were unable to detect a significant influence of demographic variables on our observed age relationships. Evidence of age-based assortative mating has been observed in birds (Marzluff and Balda 1988; Warkentine et al. 1992), and there is limited evidence in ungulates such as bison (*Bison bison*; Wolff 1988) and fallow deer (*Dama dama*; Farrell et al. 2011). While we found evidence for non-random mating, our distribution of age differences (i.e., Fig. 4) displayed a greater than expected frequency of pairings where the dam and sire were more than 1-year apart in age; in contrast to true positive assortative mating where the greatest frequency of observed difference in age would be assumed to be zero. Regardless, we believe our findings indicate age may still be an indicator of quality in mate selection resulting in mature individuals selecting for other individuals of a similar age to ensure the greatest likelihood of reproductive success (Fawcett and Johnstone 2003). In ungulates, fitness has been found to increase with age in both males and females (Clutton-Brock et al. 1982; Byers 1997; Weladji et al. 2006; Vanpé et al. 2009b; Festa-Bianchet 2012) and has also been previously observed in our study population (Newbolt et al. 2017; Swartout et al. 2023a). Females, often being the choosier sex, likely select

mature males due to age being highly correlated with larger body size, antler growth and symmetry, and dominance (Ditchkoff et al. 2001; Mysterud et al. 2004; Mainguy et al. 2008; Willis et al. 2012; Morina et al. 2018). While we observed no significant interaction between age structure and the age relationship of parental pairs, we did observe a decrease over time in the annual percentage of known sires that were 3.5 years of age or younger. It is well documented in ungulates that as male age structure matures and the sex ratio becomes balanced, fewer males participate in breeding (Bergerud 1974; Clutton-Brock et al. 1997; Røed et al. 2002; Mysterud et al. 2004; Markussen et al. 2019) due to greater breeding competition and fewer females available to breed (Ims 1988; Festa-Bianchet 2012). As our study progressed and more mature males were present, competition for mates likely increased, making it more difficult for immature males to actively participate in courtship rituals without conspecific competition (Struhsaker 1967; Ozoga and Verme 1985; Squibb 1985). As mature adults selected for other mature adults, young adult pairings that successfully recruited fawns may have been due to fewer breeding opportunities available for each sex with preferred mates and not due to active mate selection, similar to conclusions made by Farrell et al. (2011) in fallow deer. When older males are present in a population, studies have documented older females actively avoiding yearling males that are attempting courtship in white-tailed deer (Ozoga and Verme 1985), reindeer (*Rangifer tarandus*; Bergerud 1974), bison (Wolff 1998), and fallow deer (Komers et al. 1999). Active male mate choice based on the perception of age is still obscure in ungulates, but evidence in mountain goats (*Oreamnos americanus*) suggests maternal experience may have a positive influence on male mate preference (Mainguy et al. 2008) due to a greater likelihood of male reproductive success when mating with mature females. This idea was further supported by Say et al. (2003) in fallow deer; they found that males that mated with younger females often had lower reproductive success versus males that mated with older females.

Our evidence of non-random mating occurring within the population is contrary to the findings of Neuman et al. (2016). However, Neuman et al. (2016) speculated that they may have observed random mating at ACF due to the male age structure still changing within the population. Theory states that being choosy during mate selection is more common when attractive or high-quality individuals are abundant: if availability is low then choosiness should decrease (Real 1990; Crowley et al. 1991; Jennions and Petrie 1997). We did not observe a significant interaction between the age relationship of the mated pairs under varying population age structures. However, we did observe a statistically significant increase in percentage of mature pairings as the

age structure increased for both sexes while also observing a statistically significant decrease in percentage of young pairings over time. Under a young male age structure, females may have fewer preferred males to choose from resulting in a greater cost of withholding from mating opportunities by being choosy, and as a result, mate selectivity regarding age may show more variation. Several studies with white-tailed deer have documented that when females cannot be choosy (e.g., penned studies where they only have one male with which to mate) or are in a population with a very young male age structure, they choose to breed with a young male as opposed to foregoing reproduction (Haugen 1959; Ozoga and Verme 1985). However, Ozoga and Verme (1985) found that female tolerance of young courting males decreased once mature males were introduced to the population. Fertilization assurance may be a more common reproductive strategy of female white-tailed deer when availability of preferred mates is suboptimal.

We also found evidence of non-random mating for body size, supporting our overall hypothesis of individuals of similar skeletal size pairing with each other. However, we were unable to detect a significant influence of demographic variables on our observed body size relationship. Assortative mating based on physical features has largely been observed in arthropods (Ridley and Thompson 1979; Brown 1990; Jiang et al. 2013), fish (Rueger et al. 2016), reptiles (Olsson 1993), and birds (Bortolotti and Iko 1992; Delestrade 2001; Jawor et al. 2003). However, in reindeer and Soay sheep (*Ovis aries*) individuals also select mates of similar body size and weight (Røed et al. 2002; Preston et al. 2005). Multiple studies indicate females often choose larger males due to the perception of size (Bergerud et al. 1974; Robinson et al. 2006; Bowyer et al. 2007; Kie et al. 2013; Coombs et al. 2022), or the high correlation body size has with dominance over conspecifics (Townsend and Bailey 1981; Geist 1982; McElligott et al. 2001), vocalization (Charlton et al. 2007; Lemasson et al. 2015), and physical ability in withstanding the demands of the rut (Byers et al. 1994; Byers and Waits 2006). Similarly, it is well established in the literature that body size has a strong positive influence on reproductive success in females (Clutton-Brock et al. 1982; White et al. 1997; Monteith et al. 2014; Flajšman et al. 2017; Lamb et al. 2023). Evidence that males select mates based on body size is still limited, but several studies have suggested that larger, dominant males select larger females because they have greater ability to produce milk (Berger 1989; Røed et al. 2002; Preston et al. 2005). The importance of body size during mate selection likely increases as the age structure of the population increases. For example, Preston et al. (2005) found that larger male Soay sheep preferred to mate with larger females, but this selection only occurred when there were multiple females in heat during a short period of time.

We speculate that choosiness is dynamic during the breeding season, and a situational trade-off exists for males: when options are limited, as they are at the start and end of the breeding period, selectivity is low. But, during the peak of the breeding season when multiple females may be available at one time, males should be choosy (Johnstone 1997). Similarly, as the population size and age structure increased at ACF, we speculate that selectivity likely increased due to greater availability of preferential mates.

We also observed that population demographics (i.e., male and female age structure and year) had a significant influence on the relationship of lifetime body percentiles of successful parental pairs, supporting our hypothesis of demographic effects impacting the characteristics of mated pairs over time. As the age structure of both sexes increased within the population, a greater array of potential mates of varying sizes was available, which we believe resulted in an increase in choosiness of mates (Real 1990; Cotton et al. 2006; Edward and Chapman 2011; Chevalier et al. 2020). Because there is a strong positive relationship between body size and reproductive success in both sexes (Trivers 1972; Clutton-Brock 1988; Myserud et al. 2004), selecting mates with a larger body size likely improves probability of passing on genes. As a result, large individuals will likely mate with one another, and by default smaller individuals will mate with other small individuals due to limited mate availability.

We believe our findings presented thus far, regarding age and body size, provide evidence of individuals showing preference for mates with certain characteristics. However, caution is warranted in interpreting these findings as strictly positive assortative mating. In theory, 'perfect' positive assortative mating should occur when there are very minimal differences in age and body size of mates (Crespi 1989), but as mentioned previously, our results revealed some plasticity in mating preference. Other studies examining mated pairs have found similar findings (Olsson 1993; Farrell et al. 2011; Clark and Backwell 2016). For example, Olsson (1993) studying sand lizards (*Lacerta agilis*) found a mating preference for body size, and while they concluded their findings as assortative mating, they did acknowledge that large males will still mate with small females instead of withholding from mating that season. We believe it is more appropriate to interpret our findings as a general preference for mates of similar characteristics. To state differently, in a population with a mature age structure, large and mature individuals will seek mating opportunities with other large and mature individuals due to a greater chance of reproductive success, while observed pairings of small immature individuals may be due to inability to gain preferred mating opportunities and not necessarily a preference for those characteristics.

Our evidence of plasticity within the population further provides support that monopolization of females by several males is uncommon in the white-tailed deer mating system (Sorin 2004; DeYoung et al. 2009; Neuman et al. 2016; Turner et al. 2016), contrary to other polygynous ungulate mating systems (Clutton-Brock et al. 1982, 1992; Langbein and Thirgood 1989; Asa 1999; Zeng et al. 2011; Willisch et al. 2012). The tending bond mating system involves a lengthy isolation period for a female and courting male (Hirth 1977; DeYoung and Miller 2011; Airst and Lingle 2019), often allowing a greater proportion of males to gain breeding opportunities with other receptive females (Jones et al. 2011). However, we observed a decrease in young males breeding over time while still observing plasticity in age differences of parental pairs. Interestingly, in the latter half of the study, a large majority of our observations of plasticity with age involved older males mating with younger females (e.g., 3.5-year-old female successfully bred by a 9.5-year-old male). A wide variety of mature males in the population obtained breeding opportunities while effectively excluding younger age classes. However, with a mature male age structure, access to preferential females in estrus may be limited for not only younger males, but also mature males that are lower in the dominance hierarchy or are poor competitors (Festa-Bianchet 2012; Martin et al. 2016; Pero et al. 2021). As a result, these males may be less choosy and mate with a wider range of female age classes (Fawcett and Johnstone 2003).

We documented 12 cases of multiple paternity during our study involving a wide range of male age classes. The debate and documentation of multiple paternity has increased greatly in the last two decades (Wolff and Macdonald 2004; Pizzari and Wedell 2013) with growing evidence in multiple ungulates species (Endo and Doi 2002; Carling et al. 2003; Briefer et al. 2013; Vanpé et al. 2009a; Coombs et al. 2022) including white-tailed deer (DeYoung et al. 2002, 2006; Sorin 2004), however, a firm reasoning on why this phenomena occurs in ungulates is still up for debate. Alternative mating tactics (e.g., sneaky or opportunistic males) that are theorized to contribute to cases of multiple paternity have been found to be a common non-competitive strategy in younger and smaller male ungulates (Coltman et al. 2002; Willisch et al. 2012; Airst and Lingle 2020). Although these alternative mating strategies may be common in white-tailed deer and would explain some of our findings, they have yet to be documented in the field and reported in the literature. While the majority of our observed cases of multiple paternity occurred in the first 6 years of our study when the age structure was younger, there was no statistical support for this trend, possibly due to a limited sample size. We observed an average age difference of two years between sires during these events and

interestingly, just under half of our cases involved two sires that were 4.5 years of age or older. Sorin (2004) speculated that multiple paternity in white-tailed deer was likely occurring due to male displacement, where an older male displaced a younger male that successfully bred but failed to tend a female in estrus. However, we feel there exists an equally likely alternative explanation; it is entirely possible that multiple paternity also occurs when an older male successfully breeds a female but does not complete the tending process, providing an opportunity for other males to also copulate with her. Further research is warranted to better understand factors that contribute to multiple paternity.

We must acknowledge that the study population being captive may have had some influence on our findings. For example, it has been documented in white-tailed deer that population density can influence breeding behavior (Labisky and Fritzen 1998). While population density did not have a statistically significant interaction with age or body size relationships at ACF, our observed findings for mating may not represent all non-captive populations due to differences in density that may influence choosiness of mates (Crowley et al. 1991). Furthermore, while a vast proportion of each yearly cohort of deer were sampled for parentage analysis, some fawns may not have been accounted for due to mortality prior to recruitment age or due to exclusion from the dataset because their trio pair confidence for paternity assignment was below our minimum threshold of 95%. Predation of fawns has yet to be studied at ACF due to predators largely being excluded from the facility; however, bobcats and coyotes have been observed infrequently. As a result, there are breeding events that occurred during this study period that were not accounted for in our analysis.

While this study has some limitations due to the population being captive, we believe these findings further document the complexity of mating systems in ungulates while also providing an improved understanding of a species with a non-harem based polygynous mating system. We were able to document non-random mating within the population where characteristics such as age and body size have a positive influence on mate selectivity that results in successful recruitment of offspring. However, while our study was able to find that large and mature individuals generally preferred to mate with other large and mature individuals, we still observed some plasticity in mating. This warrants further research in understanding mate selectivity of this species to account for other possible unmeasured behavioral or genetic qualities (e.g., major histocompatibility complex; Santos et al. 2018) that may be highly connected to phenotypic traits (Byers and Waits 2006) and influencing mate choice. Furthermore, we observed a decreased proportion of younger males siring offspring in the population as the male age structure matured and while we speculate this is due to

some form of female selection, future studies should consider examining breeding events to improve our understanding of post-copulatory mechanisms that may impact mating success (Ivy-Israel 2019; Coombs et al. 2022).

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Author contributions Tristan J. Swartout: Conceptualization (equal); Data curation (supporting); Formal analysis (lead); Methodology (supporting); Project administration (supporting); Resources (equal); Writing original draft. Chad H. Newbolt: Data curation (lead); Funding acquisition (supporting); Methodology (supporting); Project administration (supporting); Resources (equal); Writing-review and editing. Todd D. Steury: Formal analysis (supporting); Writing-review and editing. William D. Gulsby: Writing-review and editing. Stephen S. Ditchkoff: Conceptualization (equal); Funding acquisition (lead); Methodology (supporting); Project administration (lead); Resources (equal); Supervisor (lead); Writing-review and editing.

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

Declarations

Conflict of interest None declared.

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