Influence of maternal characteristics and reproductive history on fawn recruitment in female white-tailed deer (*Odocoileus virginianus*)

and

Examination of phenotypic characteristics of successful mated pairs in white-tailed deer

by

Tristan Joseph Swartout

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Approved by

Stephen S. Ditchkoff, Chair, William R. and Fay Ireland Distinguished Professor, College of Forestry, Wildlife and Environment
William D. Gulsby, Associate Professor, College of Forestry, Wildlife and Environment
Todd D. Steury, Associate Professor, College of Forestry, Wildlife and Environment

Abstract

There still exist gaps in the literature regarding how intrinsic factors influence recruitment success and mate selectivity in white-tailed deer (*Odocoileus virginianus*). We examined a captive population of white-tailed deer from 2008 to 2019 to compare annual recruitment data to maternal age, body size, and past reproductive history. Our second objective examined characteristics of mated pairs that recruited fawns. Recruitment was significantly influenced by age, recruitment success the previous year, and an interaction between age and body size, indicating there are differences in quality of female deer and different reproductive strategies depending on age and body size. There were significant positive relationships for age and body size in mated pairs; however, large differences in age were still observed in some mated pairs. Furthermore, we documented positive assortative mating, but the mating system was dynamic, and selectivity likely changes with herd demographics.

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Chapter 1: Influence of maternal characteristics and reproductive history on recruitment in an iteroparous ungulate

Abstract

In reproductive dynamics, recruitment is a critical biological process to ensure populations remain viable. While extrinsic factors such as predation and environmental factors have been found to strongly influence recruitment, there are still literature gaps on how maternal factors such as age, body size, and past reproductive history influence recruitment. We examined a captive population of white-tailed deer (*Odocoileus virginianus*) with a known pedigree exhibiting natural breeding behavior from 2008 to 2019, and compared annual recruitment data of individuals relative to maternal age, a lifetime body size percentile (LBP), and a mother's past reproductive history. We found that recruitment success increased up to 6.5 years of age, at which it peaked, before declining in older age classes. We found that age and LBP had a significant interaction where large-bodied females had high recruitment success at younger ages and small-bodied females had high recruitment success at older ages. Interestingly, we observed that if a female successfully recruited a fawn the year prior, she recruited 1.46 times as many fawns then females that did not recruit a fawn the year prior ($P = 0.035$). We documented 40 individuals (47% of mothers) that recruited fawns in consecutive years at least once in their lifetime, and those individuals recruited 75.3% of all fawns during the study. Our findings suggest that white-tailed deer vary in reproductive strategy, dependent on body size, and a minority of females in a population successfully recruit a majority of the fawns into the breeding population.

Keywords

individual heterogeneity, life history, microsatellites, *Odocoileus virginianus*, recruitment, reproductive strategies, reproductive success

Introduction

Recruitment is a highly important biological process in population dynamics of vertebrates. While its meaning depends on the context of the study, its broad definition is defined as the addition of new individuals to a population (Gaillard et al. 2008). Most research in mammalian ecology examines reproductive recruitment, which focuses on the addition of juveniles to the breeding portion of the population. Reproductive recruitment can have much more pronounced effects on population growth and stability than other measurable parameters such as adult mortality (Gaillard et al. 2000), with population declines or little to no growth in multiple mammalian taxa largely being attributed to low reproductive recruitment (Testa 1987; Festa-Bianchet et al. 1994; Unsworth et al. 1999; Wauters et al. 2004; Reed and Slade 2008).

When examining influences on population dynamics, juvenile survival (e.g., recruitment) is often the most sensitive population parameter to extrinsic or intrinsic factors (Eberhardt 1977; Gaillard et al. 1998). In ungulates, numerous studies have examined how extrinsic factors like population density (Clutton-Brock et al. 1987; Festa-Bianchet and Jorgenson 1998; Gilbert and Raedeke 2004; Robinson et al. 2006), predation (Festa-Bianchet et al. 1994; Jarnemo and Liberg 2005; Berger and Connor 2008; Creel et al. 2011), resource availability (Julander et al. 1961; Wilson et al. 2002; McDonald 2005; Monteith et al. 2014), anthropogenic habitat alteration (Nellemann and Cameron 1998; McLoughlin et al. 2003), and weather (Simpson et al. 2007; Shalmon et al. 2021) affect recruitment, while intrinsic factors such as maternal body weight or age have been examined as to how they affect fecundity (Schwartz and Hundertmark 1993;

Birgersson and Ekvall 1997; Weladji et al. 2003; Morin et al. 2016; Flajšman et al. 2017). Similarly, in white-tailed deer (*Odocoileus virginianus*) a plethora of studies have examined effects of maternal characteristics on ability of a female to produce fawns, and findings indicate fecundity is associated positively with maternal body size and age (Verme 1969; Roseberry and Klimstra 1970; Haugen 1975; Ozoga 1987; Green et al. 2017). However, few studies have examined how these maternal characteristics influence ability to successfully recruit fawns. It has been well documented that fawn recruitment can be negatively impacted by extrinsic factors such as predation (Nelson and Mech 1986; Kilgo et al. 2010; Jackson and Ditchkoff 2013; Fortin et al. 2015; Gulsby et al. 2015), insects (Bolte et al. 1970; Logan 1973; Allen et al. 1997), disease (Carroll and Brown 1977), population density (Dusek et al. 1989; Fryxell et al. 1991; Keyser et al. 2005), food restriction during gestation and lactation (Mech 2007; Therrien et al. 2007; Aubin et al. 2022), landscape characteristics (Wright et al. 2019; Grovenburg et al. 2012), and environmental effects such as precipitation (Ginnett and Young 2000; Warbington et al. 2017) and extreme temperatures (Grovenburg et al. 2012; Michel et al. 2018). But regarding intrinsic factors, few studies have been conducted and have primarily provided only descriptive information of recruitment rates comparing yearlings to adult females (Gavin 1979; Dusek et al. 1989; Nixon and Etter 1995).

Reproductive history of a female is another intrinsic factor to consider when assessing influences on recruitment; however, literature is generally lacking on its influence on subsequent reproduction in ungulates. It is well known that lactation is a costly component of reproduction in white-tailed deer (Oftedal 1985; Robbins 1993; Hewitt 2011) and other mammals, and successful rearing of a fawn can negatively impact condition of an individual going into the next breeding season (Therrien et al. 2007; Ayotte et al. 2019). While effects on ability to recruit fawns during subsequent seasons have yet to be examined in white-tailed deer, several studies in other ungulate species have suggested that successful recruitment negatively impacts subsequent reproductive events (Clutton-Brock and Coulson 2002; Moyes et al. 2006; Martin and Festa-Bianchet 2010; Rughetti et al. 2015).

In this study, we examined reproductive patterns of adult, female white-tailed deer in a captive herd that exhibited natural breeding behavior and was exposed to conditions that would normally influence juvenile recruitment. Because of the captive aspect of the herd, we had access to detailed information concerning previous reproductive history, body measurements, and other intrinsic factors that could influence reproductive performance. Our specific objectives were to determine how maternal age, body size, and reproductive history influenced recruitment success, both individually, and in combination. We predicted female age and body size would both positively influence recruitment, while successfully recruiting a fawn would negatively influence subsequent ability to recruit fawns.

Materials and Methods

Study Area

The white-tailed deer examined in this study were from a captive herd at the Auburn Captive Facility (ACF) located in Camp Hill, Alabama. The facility was 174 ha and was surrounded by a 2.6 m fence. The population within ACF ranged annually from 71–139 individuals, and all individuals were descendants of the wild herd that was in the area when the fence was constructed in 2007. No deer were introduced to the population, and the herd was not subjected to hunting. While fawn predation was not actively documented, coyotes (*Canis latrans*) and bobcat (*Lynx rufus*) were occasionally present within ACF.

Land cover types within the facility consisted primarily of open fields (40%) for hay production and mixed forests (60%) with oak (*Quercus* spp.), sweetgum (*Liquidambar styraciflua*), hickory (*Carya* spp.), and loblolly pine (*Pinus taeda*) being the primary tree species found within the facility. Active habitat management was conducted using prescribed fire. Unburned areas contained naturally regenerated thickets consisting of blackberry (*Rubus* spp.), eastern red cedar (*Juniperus virginiana*), and Chinese privet (*Ligustrum sinense*). The predominant grass species in open fields of the facility was Bermuda grass (*Cynodon dactlyon*), but other grasses included several species of fescue (*Festuca* spp.), big bluestem (*Andropogon gerardi*), Johnson grass (*Sorghum halepense*), dallisgrass (*Paspalum dilatatum*), and bahia grass (*P. notatum*). The elevation within ACF ranged from 190–225 m above sea level, and the climate was classified as humid subtropical with a temperature throughout the year ranging from an average low of -0.5°C to an average high of 32.5°C, with annual precipitation around 137 cm (NOAA National Centers for Environmental information 2022). The facility had two creeks and natural springs that provided water. Supplemental feed and food plots were available within the fence. Three protein feeders were available ad libitum to deer all year and contained pellets that were 18% protein (Record Rack®, Nutrena Feeds; Minneapolis, MN). Food plots were planted with differing warm and cool season forages to supplement herd nutrition. Whole corn (*Zea mays*) was provided in the fall and winter through three timed feeders to attract deer for capture purposes (Newbolt et al. 2017).

Capture Techniques

From 2008 through 2013, deer were captured using two possible methods: a capture facility or cartridge-fired dart guns. The capture facility was 0.8 ha, allowed for capture of multiple individuals in one trapping effort, and is further described by Neuman et al. (2016).

Beginning in 2014, all deer were captured during mid-September to mid-March using dart guns over feeders. Dart guns were fitted with night vision scopes and fired telemetry darts using .22 caliber blanks (Kilpatrick et al. 1996). Telemetry darts (2.0 cc, type C, Pneu-Dart Inc., Williamsport, PA) contained a mixture of Telazol® (at a concentration of 125mg/ml and given at a rate of 2.2mg/kg) and Xylazine® (at a concentration of 100mg/ml given at a rate of 2.2mg/kg; Miller et al. 2003). Deer were not darted until at least 6 months of age to ensure minimal chance of capture related mortality from the tranquilizer mixture and due to the research objectives of the study focusing only on deer that had reached recruitment age (6 months of age). If a fawn was accidentally darted and later determined to not have survived to recruitment age it was excluded from further analysis.

Once a deer was observed at a feeder, a dart was shot into the hindquarter to ensure a safe and effective intramuscular injection of the sedative mixture (Kilpatrick et al. 1996). The dart was equipped with a transmitter that allowed for tracking of the immobilized deer using VHF radiotelemetry with a receiver and 3-element Yagi antenna (Kilpatrick et al. 1996). Once all samples and data were collected, Tolazoline® (1.5 mL/45.36 kg) was administered intramuscularly in the hindquarter and front shoulder to reverse sedation (Miller et al. 2004).

Data Collection

All deer were given a unique six-digit identification number and aged using the tooth replacement and wear technique (Severinghaus 1949). Deer aged ≤1.5 years old were considered to be known age because of the high accuracy of this technique with these age classes (Gee et al. 2002). We measured three skeletal body size measurements using a flexible measuring tape. The measurements were body length (tip of the snout to the proximal end of the tail, following a straight line along the backbone), chest girth (circumference of the chest directly posterior of the front legs), and hind foot length (measured from the tip of the hoof to the posterior end of the tuber calcis; Neuman et al. 2016). Ectoparasite counts (*Ixodes scapularis*, *Amblyomma Americanum, A. maculatum*, *Rhipicephalus sanguineus, Dermacenter variabilis*, *Lipoptema mazamae*) were conducted at six specific locations on sedated animals: left and right ear, left and right eye, a 10 x 10 cm location on the sternum, and the anus. Many individuals in the population were captured multiple times throughout their lifetime. This allowed for collection of up-to-date information and more accurate estimates of skeletal body size and ectoparasite counts over an individual's lifetime. To obtain a tissue sample for genetic analysis we used a notching tool to remove a 1-cm^2 tissue sample from the ear. Tissue samples were placed in a Cryule plastic cryogenic vial (Wheaton, Millville, NJ) and properly labeled for identification. All vials were then placed in a -80° C freezer for preservation as recommended by Shabihkhani et al. (2014) for long-term storage of protein and genetic samples. 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).

Microsatellite Analysis and Parentage Assignment

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). Each of the 18 loci were examined for every individual at ACF to determine allele composition. We used the software program Parentage 1.1d (Huang 2018) to estimate allelic richness (El Mousadik and Petit 1996), gene diversity (Nei 1987), and the inbreeding coefficient (Weir and Cockerham 1984). Based off genetic diversity estimates we detected significant departures from Hardy-Weinberg equilibrium at 2 of the 18 loci (Table 1.1);

however, we still included these loci in our parentage analysis due to Parentage 1.1d accounting for null alleles and inbreeding (Dakin and Avise 2004; Huang et al. 2018).

We created an annual list of candidate parents for ACF from 2008 through 2019 to account for all possible parents within ACF during a given breeding season. All females ≥6 months of age were considered candidate mothers for a year based off detection of their ear tag ID through extensive camera surveys or visual observation. Female fawns were considered candidate mothers due to prior studies documenting reproduction in fawns (Nixon 1971; Rhodes et al. 1986; Verme and Ullrey 1984; Karns et al. 2014; Neuman et al. 2016). If an individual was not detected on camera or through observation for two years, they were assumed to be deceased and removed from the candidate list.

We only assigned parentage to individuals initially captured at ≤1.5 years of age to ensure with high probability that individuals were aged correctly using the tooth replacement and wear technique (Gee et al. 2002). 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). Confidence levels were determined by Parentage 1.1d based off critical levels of the delta statistic after conducting simulations (i.e., 10,000 iterations) using our annual candidate parent lists, an inbreeding coefficient of 0.074, a loci mistype error rate of 0.01, and an assumption that 90% of our population was sampled. Maternity was only confirmed if at minimum the pair confidence level was 95%, based off similar methods in prior studies (Neuman et al. 2016; Newbolt et al. 2017; Gomes 2020; Ivy-Israel et al 2020).

Statistical Analysis

We examined annual recruitment success for all candidate mothers in the population from 2008 through 2019 relative to age, body size, and reproductive history. Due to our inability to capture each deer annually and collect body measurements every year, we calculated a lifetime body percentile and used this statistic as a surrogate for skeletal body size. Similar to Neuman et al. (2016), we pooled all total body measurements (hind foot, chest girth, and body length combined) across years, by age group, and determined an individual's ranking within that age group (e.g., an individual in the 75th percentile out of 48 individuals at 1.5 years of age). If an individual had at least two body percentiles available during its lifetime, we calculated the percentile mean to create the lifetime body percentile which was then used as the body size score for that individual's lifetime during the study period.

We used a generalized linear model with a Poisson distribution (package lme4) in the software program R (version 4.0.2; R Core Development Team 2022) to evaluate recruitment success. Reproductive data were longitudinal and, as a result, the life history of each female was examined on an annual scale (e.g., all breeding seasons a female was a candidate parent) from 2008 through 2019. Annual recruitment success, based off litter size of recruited fawns (e.g., 0,1,2,3), was the response variable and the predictor variables were Age, lifetime body percentile (LBP), and prior reproductive history. For prior reproductive history, we created two separate categorical predictor variables; examining if a female recruited a fawn the prior year (PRS) and if a female recruited a fawn during each of the two prior years (PRS2). Due to the substantial resource requirements of twin or triplet litters, we created a categorical predictor variable to account for females that recruited litter of ≥2 fawns the year prior (PL). Since the data were longitudinal, we included individual (ID) as a random effect to account for repeated measurements and to avoid potential pseudo-replication (Hurlbert 1984; Machlis et al. 1985). We also included a random effect for breeding season (Bszn) to account for annual variation in environmental factors. Each random effect had a fixed slope but varying intercepts. When examining our global model, we excluded the 2008 breeding season for females that were born in 2006 or before because of our inability to determine if that female recruited a fawn in 2007. Our continuous variables, Age and LBP, were standardized (i.e., subtracted mean and divided by the SD) through scaling and centering in the program R, and were examined with a partial likelihood ratio test to see if the inclusion of quadratic effects were appropriate (Murtaugh 2009). To examine the differences among age groups, we split age into three categorical groups: young (0.5 to 1.5 years of age), prime-age (2.5 to 6.5 years of age), and old (7.5 to 13.5 years of age) based off prior reports that prime reproductive age in female white-tailed deer is from 3–7 years of age (Verme and Ullrey 1984). We tested for collinearity by calculating variance inflation factors (VIF) and chose a maximum VIF threshold of 3 (Zuur et al. 2010). We checked for overdispersion in our models (package blemco) and tested for zero-inflation (package glmmTMB, package performance). We also tested for possible interaction terms for our predictors using a partial likelihood ratio test. When comparing life history traits and characteristics between groups of individuals we used Welch Two Sample t-tests and Two Sample z-tests.

Results

We documented 383 recruited fawns from 2008 through 2019. Because we only determined maternity for known-aged individuals (captured at ≤1.5 years of age), we were only able to determine parentage for 309 of the recruited fawns, and were able to determine maternity at the 95% confidence level for 260 of the fawns, which were used for the analysis in this study. There were 86 known mothers during the study period out of 156 candidate mothers for a total of 668 breeding season observations. There were 14 cases where a female fawn successfully recruited offspring and 24 cases of females ≥8.5 years old recruiting fawns; one female recruited a fawn at 12.5 years of age (Table 1.2). We documented 45 twin litters and 3 triplet litters, and average maternal age for twin or triplet litters was 4.92 years (SE = 0.29). We observed 12 cases of multiple paternity (i.e., ≥2 litter involves more than one sire) where the paternity of both males could be determined at a trio pair confidence level of 95%, with 6 additional cases where the trio confidence level did not meet our minimum threshold for paternity. The average maternal age during a multiple paternity event was 5.58 years (SE = 0.72).

A partial likelihood ratio test determined it was appropriate to include a quadratic effect for age ($P < 0.001$), but not LBP ($P = 0.193$), in our global model. We also determined it was appropriate to include an interaction term between our Age variables and LBP ($P = 0.016$). There was no evidence of overdispersion in our data (Dispersion Value = 0.96), and no evidence to account for zero inflation (Zero Inflation Ratio = 1.02). Before standardizing variables, collinearity was only detected for linear and quadratic Age (VIF: Age = 14.17, Age^2 = 13.76). However, we deemed this to not be a concern due to the nature of high collinearity being detected for predictor variables when quadratic effects are applied (Chatterjee and Olkin 2006). The random effect for breeding season (Bszn) was not significant and we excluded it from further analysis. The random effect for individual (ID) was also not significant but was retained in analysis due to repeated measurements.

Because some individuals did not have a score for LBP, our global model had a reduced sample size of 249 breeding season observations from 37 individuals. We found no relationship between annual fawn recruitment and LBP ($P = 0.348$), PRS ($P = 0.564$), PRS2 ($P = 0.621$), or PL ($P = 0.782$; Table 1.3). However, we did find a significant relationship between annual fawn recruitment and linear ($P = 0.045$) and quadratic Age ($P < 0.001$). Examining our interaction terms, we found annual fawn recruitment had a significant relationship with our interaction term between linear Age and LBP ($P = 0.005$), but not quadratic Age and LBP ($P = 0.415$). Running predictions based off significant terms, we found that individuals with a greater percentile score (larger body size) had greater recruitment success (predicted number of annual recruited offspring) at younger ages (0.5 to 4.5 years of age) compared to individuals with lesser percentile scores (Figure 1.1). However, we found that an inflection point occurred between 4.5 and 5.5 years of age, where older individuals (5.5 to 12.5 years of age) with lesser percentile scores had greater recruitment success than individuals with greater percentile scores (Figure 1.1). Including the random effect ID did not show significant variation within the model (Variance < 0.001).

To include individuals with no body size scores, we reran our analysis with a model excluding LBP, which resulted in 629 individual breeding season observations for 149 individuals. We found no relationship between annual fawn recruitment and PRS2 ($P = 0.948$) or PL ($P = 0.927$, Table 1.4). PRS was found to have a near-significant positive trend ($P = 0.063$) in our model, and when PRS2 was excluded to increase sample size, we found PRS had a significant positive effect on recruitment success. If a female recruited a fawn the prior year, she recruited 1.46 times as many fawns then females who did not recruit a fawn the prior year ($P = 0.035$). We also found a significant relationship between annual fawn recruitment and linear Age ($P < 0.001$) and quadratic Age ($P < 0.001$). As age increased, the annual predicted number of recruited fawns increased until it peaked at 5.5 to 6.5 years of age at 0.85 recruited fawns, then decreased (Figure 1.2). Including the random effect ID did not show significant variation within the model (Variance $= 0.010$).

When rerunning our analysis with just our Age variables we had 668 individual breeding season observations for 156 individuals. Similar to our previous findings, both linear and quadratic Age were significant ($P < 0.001$), and our predicted peak annual recruitment occurred from 5.5-6.5 years of age (Figure 1.2). When dividing Age into categorical groups, prime-age adults recruited 2.71 times as many fawns as young adults ($P < 0.001$), and old adults recruited 2.17 times as many fawns as young adults ($P < 0.001$, Table 1.5). Changing the reference group to old adults we found prime-age adults recruited 1.25 times as many fawns as old adults; however, this relationship was not statistically significant ($P = 0.192$). Including the random effect ID did not show significant variation within the model (Variance = 0.10).

Because PRS had a significant positive effect on annual fawn recruitment, we examined females who recruited fawns in consecutive seasons at least once in their lifetime (hereafter called consecutive recruiters). There were 40 known consecutive recruiters within ACF (46.5% of known mothers), with 19 of them consecutively recruiting fawns multiple times within their lifespan. Of 260 fawns, maternity of 75.3% (196 fawns) was assigned to mothers who recruited consecutively at least once in their life. Among the 36 females in ACF known to have twin or triplet litters, 28 (78%) were consecutive recruiters. Of the consecutive recruiters, 12 individuals consecutively recruited fawns at least 3 different times during their lifetime with 3 individuals recruiting at least one fawn for five straight years. There were some noteworthy individuals. Beginning at 2.5 years of age, one female recruited at least one fawn per reproductive season for 7 consecutive seasons. Another females recruited a triplet litter at 6.5 years old, then recruited a twin litter the subsequent year. From the age of 2.5 to 10.5 one female recruited nine fawns. When comparing life history traits between consecutive recruiters and other females, we found consecutive recruiters lived 5.2 years longer ($P < 0.001$), recruited the first fawn of their reproductive lifespan 0.92 years earlier ($P = 0.030$), and recruited their last fawn 4.3 years later ($P < 0.001$) than females who never recruited fawns in consecutive years (Table 1.6). Furthermore, while not statistically significant, consecutive recruiters on average had a larger

LBP (P = 0.076) and a lower parasite count (P = 0.305) than other females. When examining known males that bred with both groups, we found that sires that bred with consecutive recruiters were on average 1-year younger than sires that bred with non-consecutive recruiters (P = 0.049), and there was no difference in male LBP (P = 0.913).

Discussion

The data did not fully support our original hypothesis that age would have a positive effect on recruitment success as age increased. Instead, our findings for age are consistent with other studies in mammals indicating that reproductive performance follows a parabolic curvature: increases with age, plateaus during prime age, and begins to decrease with advanced age with the onset of senescence (Gaillard et al. 2017). In white-tailed deer, reproductive performance has been found to increase with age (Mundinger 1981; Dusek et al. 1989; Neuman et al. 2016), likely due to improvement in physical capabilities of the female, fawning site selection, predator avoidance tactics (Ozoga and Verme 1986; Mech and McRoberts 1990), and a decreased likelihood of abandoning fawns during periods of stress (Langeau and Lerg 1976; Ozoga and Verme 1982; Ozoga et al. 1982; Smith 1987). Our observation that recruitment success began to decline at 7 years of age may provide evidence for the onset of reproductive senescence (Kirkwood and Austad 2000) in white-tailed deer from the standpoint of a decline in recruitment performance. Prior studies have yet to identify reproductive senescence in white-tailed deer but have noted a decline in fecundity at 8–9 years of age (DelGiudice et al. 2007; Nixon and Mankin 2015; Ayotte et al. 2019). From the standpoint of observing different reproductive components regarding senescence, this may indicate that fertility persists longer than the ability to recruit fawns in white-tailed deer. Gaillard et al. (2017) noted several studies of mammalian taxa where reproductive declines occurred at different ages depending on what aspect of reproduction was examined (e.g., pregnancy rate vs proportion of reared offspring). Declines in recruitment in accordance with age may be due to reduced litter size at advanced ages or reproductive pauses where recruitment success occurs in alternating years; a quality over quantity tactic similar to what Green and Rothstein (1991) observed in bison (*Bison bison*). Our evidence of the possible beginnings of senescence in white-tailed deer occurring around 7 years of age is similar to findings with other ungulates: 8 years of age in reindeer (*Rangifer tarandus*; Weladji et al. 2002), 8 years of age in soay sheep (*Ovis aries*; Robinson et al. 2006), 8 years in alpine chamois (*Rupicapra rupicapra*; Morin et al. 2016), 9 years in fallow deer (*Dama dama*; San José et al. 1999), 12 years of age in moose (*Alces alces*; Ericsson et al. 2001), and 9 years of age in red deer (*Cervus elaphus*; Nussey et al. 2006).

Contrary to our original hypothesis, we did not find that body size had a significant positive effect on fawn recruitment. Instead, we found an interaction between age and LBP where larger body size had a positive impact on recruitment success at younger ages, with smaller individuals experiencing an increase in recruitment success at older ages. This suggests that white-tailed deer may undergo two separate life history strategies depending on body size, where smaller females delay reproduction to maximize skeletal growth during their first few years, whereas larger females maximize reproduction at younger ages. Attainment of maximum body size generally occurs in female white-tailed deer between 2.5 and 3.5 years of age (Ditchkoff et al. 1997, Strickland and Demarais 2000). Prior to that, a female undergoes a tradeoff: reproduce at the cost of somatic growth or delaying reproductive investment to ensure maximize growth and future residual reproductive value (Fisher 1930, Williams 1966; Pianka 1976). In support of our findings, multiple studies in ungulates have found that increased body mass in young adult females resulted in increased reproduction due to an improved ability in handling the costs of reproduction (Hewison 1996; Sand 1996; Monteith et al. 2014; Flajšman et al. 2017; Festa-Bianchet et al. 2019). Furthermore, in white-tailed deer, Michel et al. (2019) found that heavier primiparous mothers were able to allocate more resources towards reproduction through increased litter size and fawn weight relative to lighter primiparous mothers. Interestingly, we observed a decrease in recruitment success after 4.5 years of age in larger individuals. In iteroparous animals, high reproductive success at a young age may increase the onset of reproductive and survival senescence due to reduced subsequent body condition (Williams 1966; Stearns 1992) and accumulation of physiological damage and deterioration (Kirkwood 1977; Kirkwood and Rose 1991; McNamara et al. 2009). This follows a live fast, die young reproductive strategy (Bonduriansky et al. 2008), which in ungulates is more commonly described for males (Robinson et al. 2006; Lemaître et al. 2018; Gomes et al. 2021). Most evidence for decreased survival and an increased rate of reproductive senescence in females has been observed in birds (Gustafsson and Pärt 1990; Reid et al. 2003; Charmantier et al. 2006; Reed et al. 2008**)** and short-lived mammals (Descamps et al. 2006; Rubach et al. 2020) but several studies have observed this in iteroparous mammals (Reiter and Le Boeuf 1991; Hayward et al. 2014), including red deer (Nussey et al. 2006). Unfortunately, we did not measure body mass in our study and were unable to determine if there was a decline in condition past 4.5 years of age that may have contributed to decreased recruitment.

Small-bodied individuals may undergo reproductive restraint (Curio 1983) at younger ages to ensure future reproductive value and their own survival while still undergoing somatic growth. Reproductive restraint follows a conservative strategy that has been observed in multiple ungulates through delaying age of primiparity or alternating years of reproductive success (Sæther and Haagenrud 1983; Green and Rothstein 1991; Kirkpatrick et al. 1993; Cameron 1994;

White et al. 1997). Therrien et al. (2007) found that female white-tailed deer with a restricted diet adopted a conservative strategy by favoring their own survival over that of their fawns. However, delaying age of primiparity to prolong body size growth has been found in other taxa to have a negative effect on lifetime reproductive success (Lindström 1999; Descamps et al. 2006; Marcil-Ferland et al. 2013). As a result, once maximized body size is attained, smaller individuals need to attempt to maximize lifetime fitness through an increase in recruitment success.

We observed that prior recruitment success (PRS) had a positive effect on subsequent recruitment, contrary to our original hypothesis. The nutritional demands and resource expenditure of rearing offspring is extremely high (Andersson et al. 1980; Clutton-Brock et al. 1989), often leaving a female in suboptimal condition when entering the subsequent breeding season (Stearns 1992). Therrien et al. (2007) found that if a female white-tailed deer weaned a fawn the prior year, they gained less mass per day compared to females that did not, leading them to speculate that costs of prior reproduction could negatively impact subsequent reproduction. Similarly, reproductive declines have been observed after successfully rearing offspring the prior year in alpine ibex (*Capra ibex*; Rughetti et al. 2015), elk (*Cervus elaphus*; Morano et al. 2013), moose (Testa 2004), and red deer (Clutton-Brock and Coulson 2002; Moyes et al. 2006). However, similar to our findings, positive effects of prior reproduction have been observed in alpine chamois (Tettamanti et al. 2015), bighorn sheep (*Ovis canadensis*; Festa-Bianchet 1989; Hamel et al. 2009*a*), mountain goat (Hamel et al. 2009*a*), northern elephant seal (*Mirounga angustirostris*; Le Boeuf et al. 2019), pronghorn (*Antilocapra americana*; Byers 1997), reindeer (Weladji et al. 2008), roe deer (*Capreolus capreolus*; Hamel et al. 2009*a*), and soay sheep (*Ovis aries*; Clutton-Brock and Coulson 2002).

We believe that the ability to consecutively recruit offspring is due to individual differences in phenotypic quality. Hamel et al. (2009*a*) found in their multispecies study that high-quality individuals consistently had a greater likelihood of reproductive success in consecutive seasons while low-quality individuals continued to perform poorly. Our data indicates that our population contains high-quality and low-quality mothers, similar to findings in multiple taxa (Clutton-Brock 1988; McCleery et al. 2008; Moyes et al. 2009; Kennamer et al. 2016). While we were unable to detect individual heterogeneity when using random effects, we observed significant differences in life history traits between groups; specifically, longevity and age of primiparity. The debate on what causes variation in individual fitness is still ongoing (Cam et al. 2016). Several studies in iteroparous mammals hypothesize that longevity brings maternal experience, in turn improving a mother’s quality (Byers 1997; Weladji et al. 2006; McLean et al. 2019); however, further research is warranted before any conclusion can be made on why we have high-quality individuals within our study population. We recommend future studies examine individual heterogeneity when examining lifetime reproductive success in regard to differences in life history traits, similar to methods in other studies (Hamel et al. 2009*a*; Hamel et al. 2009*b*; Desprez et al. 2018; McLean et al. 2019).

An important consideration regarding our data is the ad libitum availability of supplemental feed in our study population, and the potential influence on body condition and recovery following successful recruitment of fawns. It is possible that the positive association between current and subsequent fawn recruitment was somewhat an artifact of the nutritional environment. For example, declines in fecundity and recruitment the subsequent year have been observed in resource-limited populations of alpine ibex, caribou, and bighorn sheep (Cameron 1994; Festa-Bianchet et al. 1998; Martin and Festa-Bianchet 2010; Rughetti et al. 2015). In contrast, other populations of the same species that had access to adequate resources reported results similar to ours (Festa-Bianchet 1989; Toügo et al. 2002; Weladji et al. 2008; Hamel et al. 2009*a*). Because the ability of a mother to overcome the challenges of consecutively recruiting offspring in successive years is likely positively influenced by availability of supplemental feed, we speculate that our ability to detect trends associated with the quality of a mother was magnified. We believe that quality differences among mothers becomes exaggerated in these situations. However, despite supplemental feed being available year-round to all the deer in our study, only <50% of mothers consecutively recruited fawns during their lifetime. This indicates to us that heterogeneity in quality among individuals is a real thing, and a subset of high-quality individuals in the population annually recruit a large majority of the fawns.

Literature Cited

Andersson M, Wiklund CG, Rundgren H (1980) Parental defense of offspring: a model and an example. Animal Behavior 28:536-542

Allen CR, Demarais S, Lutz RS (1997) Effects of red imported fire ants on recruitment of white-tailed deer fawns. The Journal of Wildlife Management 61:911-916

Anderson JD, Honeycutt RL, Gonzales RA et al (2002) Development of microsatellite DNA markers for the automated genetic characterization of white-tailed deer populations. Journal of Wildlife Management 66:67-74

Aubin GR, Nye CC, Rohm JH et al (2022) Survival of white-tailed deer fawns on Marine Corps Base Quantico. The Journal of Wildlife Management. 86:e22180

Ayotte P, Simard MA, Côté SD (2019) Reproductive plasticity of female white-tailed deer at high density and under harsh climatic conditions. Oecologia 189:661-673

Berger KM, Conner MM (2008) Recolonizing wolves and mesopredator suppression of coyotes: impacts on pronghorn population dynamics. Ecological applications 18:599-612

Birgersson B, Ekvall K (1997) Early growth in male and female fallow deer fawns. Behavioral Ecology 8:493-499

Bolte JR, Hair JA, Fletcher J (1970) White-tailed deer mortality following tissue destruction induced by lone star ticks. The Journal of Wildlife Management 34:546-552

Bonduriansky R, Maklakov A, Zajitschek F et al. (2008) Sexual selection, sexual conflict and the evolution of ageing and life span. Functional Ecology, 22:443-453

Byers JA (1997) American pronghorn: social adaptations and the ghosts of predators past. University of Chicago Press, Chicago

Cam E, Aubry LM, Authier M (2016) The conundrum of heterogeneities in life history studies. Trends in Ecology & Evolution 31:872-886

Cameron RD (1994) Reproductive pauses by female caribou. Journal of Mammalogy 75:10-13

Carroll BK, Brown DL (1977). Factors affecting neonatal fawn survival in southern-central Texas. The Journal of Wildlife Management 41:63-69

Charmantier A, Perrins C, McCleery RH et al (2006) Quantitative genetics of age at reproduction in wild swans: support for antagonistic pleiotropy models of senescence. Proceedings of the National Academy of Sciences 103:6587-6592

Chatterjee S, Olkin I (2006) Nonparametric estimation for quadratic regression. Statistics & probability letters 76:1156-1163

Chitwood MC, Lashley MA, Kilgo JC et al (2015) Do biological and bedsite characteristics influence survival of neonatal white-tailed deer?. PloS one 10:e0119070

Clutton-Brock TH (1988) Reproductive success: studies of individual variation in contrasting breeding systems. University of Chicago Pres, Chicago

Clutton-Brock TH, Albon SD, Guinness FE (1989) Fitness costs of gestation and lactation in wild mammals. Nature 337:260-262

Clutton–Brock TH, Coulson T (2002) Comparative ungulate dynamics: the devil is in the detail. Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences 357:1285-1298

Clutton-Brock TH, Major M, Albon SD, Guinness FE (1987) Early development and population dynamics in red deer. I. Density-dependent effects on juvenile survival. The Journal of Animal Ecology 56:53-67

Creel S, Christianson DA, Winnie Jr JA (2011) A survey of the effects of wolf predation risk on pregnancy rates and calf recruitment in elk. Ecological Applications 21:2847-2853

Curio E (1983) Why do young birds reproduce less well?. Ibis 125:400-404

Dakin EE, Avise JC (2004) Microsatellite null alleles in parentage analysis. Heredity 93:504-509

DelGiudice GD, Lenarz MS, Powell MC (2007) Age-specific fertility and fecundity in northern free-ranging white-tailed deer: evidence for reproductive senescence?. Journal of Mammalogy 88:427-435

Descamps S, Boutin S, Berteaux D (2006) Best squirrels trade a long life for an early reproduction. Proceedings of the Royal Society B: Biological Sciences 273:2369-2374

Desprez M, Gimenez O, McMahon CR et al (2018) Optimizing lifetime reproductive output: Intermittent breeding as a tactic for females in a long-lived, multiparous mammal. Journal of Animal Ecology 87:199-211

Ditchkoff SS, Welch Jr ER, Starry WR et al (1997) Quality deer management at the McAlester Army Ammunition Plant: a unique approach. Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies 51:389-399

Dusek GL, MacKie RJ, Herriges Jr JD et al (1989) Population ecology of white-tailed deer along the lower Yellowstone River. Wildlife Monographs 104:3-68

Eberhardt LL (1977) “Optimal" Management Policies for Marine Mammals. Wildlife Society Bulletin 5:162-169

El Mousadik A, Petit RJ (1996) High level of genetic differentiation for allelic richness among populations of the argan tree [*Argania spinosa* (L.) Skeels] endemic to Morocco. Theoretical and Applied Genetics 92:832–839

Ericsson G, Wallin K, Ball JP et al (2001) Age-related reproductive effort and senescence in free-ranging moose, *Alces alces*. Ecology 82:1613-1620

Festa-Bianchet M (1989) Individual differences, parasites, and the costs of reproduction for bighorn ewes (*Ovis canadensis*). The Journal of Animal Ecology 58:785-795

Festa-Bianchet M, Côté SD, Hamel S et al (2019) Long-term studies of bighorn sheep and mountain goats reveal fitness costs of reproduction. Journal of Animal Ecology 88:1118-1133

Festa-Bianchet M, Gaillard JM, Jorgenson JT (1998) Mass-and density-dependent reproductive success and reproductive costs in a capital breeder. The American Naturalist 152:367-379

Festa-Bianchet M, Jorgenson JT (1998) Selfish mothers: reproductive expenditure and resource availability in bighorn ewes. Behavioral Ecology 9:144-150

Festa-Bianchet M, Urquhart M, Smith KG (1994) Mountain goat recruitment: kid production and survival to breeding age. Canadian Journal of Zoology 72:22-27

Fisher RA (1930) The genetical theory of natural selection. Oxford University Press, Oxford

Flajšman K, Jerina K, Pokorny B (2017) Age-related effects of body mass on fertility and litter size in roe deer. PloS one 12:e0175579

Fortin NL, Pekins PJ, Gustafson KA (2015) Productivity measures of white-tailed deer in New Hampshire: assessing reduced recruitment. Wildlife Society Bulletin 39:56-64

Fryxell JM, Hussell DJ, Lambert AB et al (1991) Time lags and population fluctuations in white-tailed deer. The Journal of Wildlife Management 55:377-385

Gaillard JM, Coulson T, Festa-Bianchet M (2008) Recruitment. In: Jørgensen SE, Fath BD (eds) Encyclopedia of ecology. Elsevier, Amsterdam, pp 2982–2986

Gaillard JM, Festa-Bianchet M, Yoccoz NG (1998) Population dynamics of large herbivores: variable recruitment with constant adult survival. Trends in ecology & evolution 13:58-63

Gaillard JM, Festa-Bianchet M, Yoccoz NG et al (2000) Temporal variation in fitness components and population dynamics of large herbivores. Annual Review of ecology and Systematics 31:367-393

Gaillard JM, Garratt M, Lemaître JF (2017) Senescence in mammalian life-history traits. In: Shefferson RP, Jones OR, Salguero-Gómez R (eds) The evolution of senescence in the tree of life. Cambridge University Press, Cambridge, pp 126–155

Gavin TA (1979) Population ecology of the Columbian white-tailed deer. Dissertation, Oregon State University

Gee KL, Holman JH, Causey MK et al (2002) Aging white-tailed deer by tooth replacement and wear: a critical evaluation of a time-honored technique. Wildlife Society Bulletin 30:387-393

Gilbert BA, Raedeke KJ (2004) Recruitment dynamics of black-tailed deer in the western Cascades. The Journal of Wildlife Management 68:120-128

Ginnett TF, Young ELB (2000) Stochastic recruitment in white-tailed deer along an environmental gradient. The Journal of Wildlife Management 64:713-720

Gomes MA (2020) Patterns of Testosterone in White-tailed Deer and their Relationship to Reproductive Success. Thesis, Auburn University

Gomes MA, Ditchkoff SS, Zohdy S et al (2021) Patterns of testosterone in male white-tailed deer (*Odocoileus virginianus*): Seasonal and lifetime variation. Ecology and Evolution 11:5320-5330

Green ML, Kelly AC, Satterthwaite-Phillips D et al (2017) Reproductive characteristics of female white-tailed deer (*Odocoileus virginianus*) in the Midwestern USA. Theriogenology 94:71-78

Green WC, Rothstein A (1991) Trade-offs between growth and reproduction in female bison. Oecologia 86:521-527

Grovenburg TW, Klaver RW, Jenks JA (2012) Survival of white-tailed deer fawns in the grasslands of the northern Great Plains. The Journal of Wildlife Management 76:944-956

Gulsby WD, Killmaster CH, Bowers JW et al (2015) White-tailed deer fawn recruitment before and after experimental coyote removals in central Georgia. Wildlife Society Bulletin 39:248-255

Gustafsson L, Pärt T (1990) Acceleration of senescence in the collared flycatcher *Ficedula albicollis* by reproductive costs. Nature 347:279-281

Hamel S, Côté SD, Gaillard JM et al (2009*a*) Individual variation in reproductive costs of reproduction: High-quality females always do better. Journal of Animal Ecology 78:143-151

Hamel S, Gaillard JM, Festa-Bianchet M et al (2009*b*) Individual quality, early-life conditions, and reproductive success in contrasted populations of large herbivores. Ecology 90:1981-1995

Haugen AO (1975) Reproductive performance of white-tailed deer in Iowa. Journal of Mammalogy 56:151-159

Hayward AD, Mar KU, Lahdenperä M et al (2014) Early reproductive investment, senescence and lifetime reproductive success in female Asian elephants. Journal of Evolutionary Biology 27:772-783

Hewison AJM (1996) Variation in the fecundity of roe deer in Britain: effects of age and body weight. Acta theriologica 41:187-198

Hewitt DG (2011) Nutrition. In: Hewitt DG (ed) Biology and management of white-tailed deer. CRC Press, Boca Raton, Florida, pp 75-105

Huang K (2018) Parentage V1.1 Manual. Northwest University. https://github.com/huangkang1987/parentage/raw/master/parentage_1.1d.zip

Huang K, Mi R, Dunn DW, et al (2018) Performing parentage analysis in the presence of inbreeding and null alleles. Genetics 210:1467-1481

Hurlbert SH (1984) Pseudoreplication and the design of ecological field experiments. Ecological monographs 54:187-211

Ivy-Israel N, Moore CE, Schwartz TS et al (2020) Characterization of two MHC II genes (DOB, DRB) in white-tailed deer (*Odocoileus virginianus*). BMC genetics 21:1-7

Jackson AM and Ditchkoff SS (2013) Survival estimates of white-tailed deer fawns at Fort Rucker, Alabama. American Midland Naturalist 170:184-190

Jarnemo A, Liberg O (2005) Red fox removal and roe deer fawn survival—a 14-year study. The Journal of Wildlife Management 69:1090-1098

Jones AG, WR Arden (2003) Methods of parentage analysis in natural populations. Molecular Ecology 12:2511-2523

Julander O, Robinette WL, Jones DA (1961) Relation of summer range condition to mule deer herd productivity. The Journal of Wildlife Management 25:54-60

Karns GR, Holland AM, Steury TD et al (2014) Maternal life history of white-tailed deer: factors affecting fetal sex allocation, conception timing, and senescence. Evolutionary Ecology Research 16:165-178

Kennamer RA, Hepp GR, Alexander BW (2016) Effects of current reproductive success and individual heterogeneity on survival and future reproductive success of female Wood Ducks. The Auk: Ornithological Advances 133:439-450

Keyser PD, Guynn Jr DC, Hill Jr HS (2005) Population density-physical condition relationships in white-tailed deer. The Journal of Wildlife Management 69:356-365.

Kilgo JC, Ray HS, Ruth C et al (2010) Can coyotes affect deer populations in southeastern North America?. The Journal of Wildlife Management 74:929-933

Kilpatrick, HJ, DeNicola AJ, Ellingwood MR (1996) Comparison of standard and transmitter-equipped darts for capturing white-tailed deer. Wildlife Society Bulletin 24:306–310

Kirkpatrick JF, Gudermuth DF, Flagan RL et al (1993) Remote monitoring of ovulation and pregnancy of Yellowstone bison. The Journal of Wildlife Management 57:407-412

Kirkwood TB (1977) Evolution of ageing. Nature 270:301-304

Kirkwood TB, Rose MR (1991) Evolution of senescence: late survival sacrificed for reproduction. Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences 332:15-24

Kirkwood TB, and Austad SN (2000) Why do we age?. Nature 408:233-238

Langenau Jr EE, Lerg JM (1976) The effects of winter nutritional stress on maternal and neonatal behavior in penned white-tailed deer. Applied Animal Ethology 2:207-223

Le Boeuf B, Condit R, Reiter J. (2019) Lifetime reproductive success of northern elephant seals (*Mirounga angustirostris*). Canadian Journal of Zoology 97:1203-1217

Lemaître JF, Cheynel L, Douhard F et al. (2018) The influence of early-life allocation to antlers on male performance during adulthood: Evidence from contrasted populations of a large herbivore. Journal of Animal Ecology 87:921-932

Lindström J (1999) Early development and fitness in birds and mammals. Trends in ecology & evolution 14:343-348

Logan T (1973) Study of white-tailed deer fawn mortality on Cookson Hills deer refuge eastern Texas. Proceedings South Eastern Association Game and Fish Commissioners 26:27-38

Machlis L, Dodd PW, Fentress JC (1985) The pooling fallacy: problems arising when individuals contribute more than one observation to the data set. Zeitschrift für Tierpsychologie. 68:201-214

Marcil-Ferland D, Festa-Bianchet M, Martin AM et al (2013) Despite catch-up, prolonged growth has detrimental fitness consequences in a long-lived vertebrate. The American Naturalist 182:775-785

Martin JG, Festa-Bianchet M (2010) Bighorn ewes transfer the costs of reproduction to their lambs. The American Naturalist 176:414-423

McCleery RH, Perrins CM, Sheldon BC et al (2008) Age-specific reproduction in a long-lived species: the combined effects of senescence and individual quality. Proceedings of the Royal Society B: Biological Sciences 275:963-970

McDonald DT (2005) Factors affecting pronghorn fawn recruitment in central Arizona. Dissertation, Texas Tech University

McLean EM, Archie EA, Alberts SC (2019) Lifetime fitness in wild female baboons: trade-offs and individual heterogeneity in quality. The American Naturalist 194:745-759

McLoughlin PD, Dzus E, Wynes BO et al (2003) Declines in populations of woodland caribou. The Journal of Wildlife Management 67:755-761

McNamara JM, Houston AI, Barta Z et al (2009) Deterioration, death and the evolution of reproductive restraint in late life. Proceedings of the Royal Society B: Biological Sciences 276:4061-4066

Mech LD (2007) Femur-marrow fat of white-tailed deer fawns killed by wolves. The Journal of Wildlife Management 71:920-923

Mech LD, McRoberts RE (1990) Survival of white-tailed deer fawns in relation to maternal age. Journal of Mammalogy 71:465-467.

Michel ES, Jenks JA, Kaskie KD et al (2018) Weather and landscape factors affect white-tailed deer neonate survival at ecologically important life stages in the Northern Great Plains. PLoS One 13:e0195247

Michel ES, Demarais S, Strickland BK et al (2019) Body mass influences maternal allocation more than parity status for a long-lived cervid mother. Journal of Mammalogy 100:1459-1465

Miller BF, Muller LI, Storms TN et al (2003) A comparison of carfentanil/xylazine and Telazol®/xylazine for immobilization of white-tailed deer. Journal of Wildlife Diseases 39:851-858

Miller BF, Muller LI, Doherty T et al (2004) Effectiveness of antagonists for tiletamine-zolazepam/xylazine immobilization in female white-tailed deer. Journal of Wildlife Diseases 40:533-537

Monteith KL, Bleich VC, Stephenson TR et al (2014) Life-history characteristics of mule deer: effects of nutrition in a variable environment. Wildlife Monographs 186:1-62

Morano S, Stewart KM, Sedinger JS et al (2013) Life-history strategies of North American elk: trade-offs associated with reproduction and survival. Journal of Mammalogy 94:162-172

Morin A, Rughetti M, Rioux-Paquette S et al (2016) Older conservatives: reproduction in female Alpine chamois (*Rupicapra rupicapra*) is increasingly risk-averse with age. Canadian Journal of Zoology 94:311-321

Moyes K, Coulson T, Morgan BJ et al (2006) Cumulative reproduction and survival costs in female red deer. Oikos 115:241-252

Moyes K, Morgan BJ, Morris A et al (2009) Exploring individual quality in a wild population of red deer. Journal of Animal Ecology 78:406-413

Mundinger JG (1981) White-tailed deer reproductive biology in the Swan Valley, Montana. The Journal of Wildlife Management 45:132-139

Murtaugh PA (2009) Performance of several variable-selection methods applied to real ecological data. Ecology letters 12:1061-1068

Nei, M (1987) Molecular evolutionary genetics. Columbia University Press, New York, New York

Nixon CM, Etter D (1995) Maternal age and fawn rearing success for white-tailed deer in Illinois. American Midland Naturalist 133:290-297

Nixon CM, Mankin PC (2015) Effects of senescence on female white-tailed deer in Illinois. Transactions of the Illinois State Academy of Science 108:35-37

Nellemann C, Cameron RD (1998) Cumulative impacts of an evolving oil-field complex on the distribution of calving caribou. Canadian Journal of Zoology 76:1425-1430

Nelson ME, Mech LD (1986) Mortality of white-tailed deer in northeastern Minnesota. The Journal of Wildlife management 50:691-698

Neuman TJ, Newbolt CH, Ditchkoff SS et al (2016) Microsatellites reveal plasticity in reproductive success of white-tailed deer. Journal of Mammalogy 97:1441-1450

Newbolt CH, Acker PK, Neuman TJ et al (2017) Factors influencing reproductive success in male white-tailed deer. The Journal of Wildlife Management 81:206-217

Nixon CM (1971) Productivity of white-tailed deer in Ohio. The Ohio Journal of Science 71:217-225

NOAA National Centers for Environmental information (2022) National Oceanic and Atmospheric Administration. Available from https://www.ncei.noaa.gov/ (accessed April 2022)

Nussey DH, Kruuk LE, Donald A et al (2006) The rate of senescence in maternal performance increases with early-life fecundity in red deer. Ecology Letters 9:1342-1350

Oftedal OT (1985) Pregnancy and lactation. In: Hudson RJ, White RG (eds) The Bioenergetics of Wild Herbivores. CRC Press Boca Raton, Florida, pp 215-238

Ozoga JJ (1987) Maximum fecundity in supplementally-fed northern Michigan white-tailed deer. Journal of Mammalogy 68:878-879

Ozoga JJ, Verme LJ (1982) Physical and reproductive characteristics of a supplementally-fed white-tailed deer herd. The Journal of Wildlife Management 46:281-301

Ozoga JJ, Verme LJ (1986) Relation of maternal age to fawn-rearing success in white-tailed deer. The Journal of Wildlife Management 50:480-486

Ozoga JJ, Verme LJ, Bienz CS (1982) Parturition behavior and territoriality in white-tailed deer: impact on neonatal mortality. The Journal of Wildlife Management 46:1-11

R Development Core Team (2014) R: A language and environment for statistical computing. R Foundation for Statistical Computing. http://www.R-project.org/

Reed AW, Slade NA (2008) Density-dependent recruitment in grassland small mammals. Journal of Animal Ecology 77:57-65

Reed TE, Kruuk LE, Wanless S et al (2008) Reproductive senescence in a long-lived seabird: rates of decline in late-life performance are associated with varying costs of early reproduction. The American Naturalist 171:E89-101

Reid JM, Bignal EM, Bignal S et al (2003) Age-specific reproductive performance in red-billed choughs *Pyrrhocorax pyrrhocorax*: patterns and processes in a natural population. Journal of Animal Ecology 72:765-776

Reiter J, Le Boeuf BJ (1991) Life history consequences of variation in age at primiparity in northern elephant seals. Behavioral Ecology and Sociobiology 28:153-160

Rhodes Jr OE, Novak JM, Smith MH et al (1986) Assessment of fawn breeding in a South Carolina deer herd. Proceedings Annual Conference Southeast Association Fish and Wildlife Agencies 40:430-437

Robbins CT (1993) Wildlife feeding and nutrition. Academic Press, New York

Robinson MR, Pilkington JG, Clutton-Brock TH et al (2006) Live fast, die young: trade-offs between fitness components and sexually antagonistic selection on weaponry in Soay sheep. Evolution 60:2168-2181

Roseberry JL, Klimstra WD (1970) Productivity of white-tailed deer on crab orchard national wildlife refuge. The Journal of Wildlife Management 34:23-28

Rubach KK, Dobson FS, Zinner B et al (2020) Comparing fitness measures and the influence of age of first reproduction in Columbian ground squirrels. Journal of Mammalogy 101:1302-1312

Rughetti M, Dematteis A, Meneguz PG et al (2015) Age-specific reproductive success and cost in female Alpine ibex. Oecologia 178:197-205

Sæther BE, Haagenrud H (1983) Life history of the moose (*Alces alces*): fecundity rates in relation to age and carcass weight. Journal of Mammalogy 64:226-232

Sand H (1996) Life history patterns in female moose (*Alces alces*): the relationship between age, body size, fecundity and environmental conditions. Oecologia 106:212-220

San José C, Braza F, Aragón S (1999) The effect of age and experience on the reproductive performance and prenatal expenditure of resources in female fallow deer (*Dama dama*). Canadian Journal of Zoology 77:1717-1722

Schwartz CC, Hundertmark KJ (1993) Reproductive characteristics of Alaskan moose. The Journal of Wildlife Management 54:454-468

Severinghaus CW (1949) Tooth development and wear as criteria of age in white-tailed deer. Journal of Wildlife Management 13:195–216

Shabihkhani M, Lucey GM, Wei B et al (2014) The procurement, storage, and quality assurance of frozen blood and tissue biospecimens in pathology, biorepository, and biobank settings. Clinical biochemistry 47:258-266

Shalmon B, Sun P, Wronski T (2021) Early and late fawn mortality in a remnant population of Arabian gazelles (*Gazella arabica*). Mammalian Biology 101:709-714

Simpson DC, Harveson LA, Brewer CE et al (2007) Influence of precipitation on productivity and abundance of pronghorn in west Texas. The Journal of Wildlife Management 71:906-910

Smith WP (1987) Maternal defense in Columbian white-tailed deer: when is it worth it?. The American Naturalist. 130:310-316

Stearns SC (1992) The evolution of life histories. Oxford University Press, Oxford

Strickland BK, Demarais S (2000) Age and regional differences in antlers and mass of white-tailed deer. The Journal of Wildlife Management 64:903-911

Testa JW (1987) Juvenile survival and recruitment in a population of Weddell seals (*Leptonychotes weddellii*) in McMurdo Sound, Antarctica. Canadian Journal of Zoology 65:2993-2997

Testa JW (2004) Population dynamics and life history trade-offs of moose (*Alces alces*) in south-central Alaska. Ecology, 85:1439–1452

Tettamanti F, Grignolio S, Filli F et al (2015) Senescence in breeding success of female Alpine chamois (*Rupicapra rupicapra*): the role of female quality and age. Oecologia 178:187-195

Therrien JF, Côté SD, Festa-Bianchet M et al (2007) Conservative maternal care in an iteroparous mammal: a resource allocation experiment. Behavioral Ecology and Sociobiology 62:193-199

Toïgo C, Gaillard JM, Gauthier D et al (2002) Female reproductive success and costs in an alpine capital breeder under contrasting environments. Ecoscience 9:427-433

Unsworth JW, Pac DF, White GC, Bartmann RM (1999) Mule deer survival in Colorado, Idaho, and Montana. The Journal of Wildlife Management 63:315-326

Verme LJ (1969) Reproductive patterns of white-tailed deer related to nutritional plane. The Journal of Wildlife Management 33:881-887

Verme LJ, Ullrey DE (1984) Physiology and Nutrition. In: Halls LK (ed) White-tailed deer: ecology and management. Stackpole, Harrisburg, Pennsylvania, pp 91-118

Warbington CH, Van Deelen TR, Norton AS (2017) Cause-specific neonatal mortality of white-tailed deer in Wisconsin, USA. The Journal of Wildlife Management 81:824-833

Wauters LA, Matthysen E, Adriaensen F et al (2004) Within-sex density dependence and population dynamics of red squirrels *Sciurus vulgaris*. Journal of animal ecology 73:11-25

Weir BS, Cockerham CC (1984) Estimating F-statistics for the analysis of population structure. Evolution 38:1358–1370

White RG, Rowell JE, Hauer WE (1997) The role of nutrition, body condition and lactation on calving success in muskoxen. Journal of Zoology 243:13-20

Williams GC (1966) Adaptation and natural selection. Princeton University Press, Princeton

Wilson GA, Olson W, Strobeck C (2002) Reproductive success in wood bison (*Bison bison athabascae*) established using molecular techniques. Canadian Journal of Zoology 80:1537-1548

Weladji RB, Gaillard JM, Yoccoz NG et al (2006) Good reindeer mothers live longer and become better in raising offspring. Proceedings of the Royal Society B: Biological Sciences 273:1239-1244

Weladji RB, Loison A, Gaillard JM et al (2008) Heterogeneity in individual quality overrides costs of reproduction in female reindeer. Oecologia 156:237-247

Weladji RB, Mysterud, A, Holand Ø et al (2002) Age-related reproductive effort in reindeer (*Rangifer tarandus*): evidence of senescence. Oecologia 131:79-82

Wright CA, McRoberts JT, Wiskirchen KH et al (2019) Landscape-scale habitat characteristics and neonatal white-tailed deer survival. The Journal of Wildlife Management 83:1401-1414

Zuur AF, Ieno EN, Elphick CS (2010) A protocol for data exploration to avoid common statistical problems. Methods in ecology and evolution. 1:3-14

Table 1.1. Microsatellites used for parentage analysis for white-tailed deer from 2008 to 2019 at the Auburn Captive Facility, Camp Hill, Alabama.

Locus	Samples	Allelic Richness	Gene Diversity[b]	F_{IS}	P[c]
Cervid1	468	14	0.87	0	1
L	467	10	0.78	0.06	0.66
BM6506	468	12	0.87	-0.01	1
N	468	16	0.87	0.19	1
INRA011	443	8	0.31	-0.06	1
BM6438	468	10	0.78	0.01	1
O	468	9	0.66	0	0.99
BL25	467	5	0.48	0	0.94
K	467	4	0.14	0.04	1
Q	466	15	0.82	0.1	1
D	465	10	0.72	0.18	0.6
OAR	468	12	0.79	-0.01	1
P	463	8	0.8	0.18	<0.001
S	466	17	0.89	0.01	1
RT5	352[a]	11	0.76	-0.04	1
RT7	352[a]	13	0.85	0.02	1
RT13	346[a]	12	0.81	0.32	<0.001
BL42	332[a]	9	0.78	-0.06	0.92

[a] Smaller sample size due to locus not being examined at ACF till 2014.

[b] Based off the Polymorphic Information Content Value.

[c] P value for Chi-Square test for deficit of homozygosity.

Table 1.2. Age-specific recruitment of fawns with maternal-known parentage at the Auburn Captive Facility from 2008 to 2019.

Age Class	Potential Mothers[a]	Known Mothers[b]	Recruited Fawns
0.5	126	14	15
1.5	107	28	29
2.5	84	35	41
3.5	77	34	43
4.5	65	22	34
5.5	56	23	30
6.5	43	14	20
7.5	35	15	20
8.5	26	8	11
9.5	21	10	11
10.5	13	2	2
11.5	9	3	3
12.5	5	1	1
13.5	1	0	0

[a] Based off candidate mother lists for each year.

[b] Based of Parentage 1.1d with a minimum confidence threshold of 95%.

Table 1.3. Generalized linear model results comparing annual recruitment success to lifetime body percentile (LBP), prior recruitment success for the past year (PRS) and past two years (PRS2), if the prior litter had >1 fawns (PL), linear and quadratic age, and a interaction term between lifetime body percentile and age (LBP:Age, LBP:Age^2). Data obtained from white-tailed deer at the Auburn Captive Facility from 2008 to 2019.

Parameter	Value[a]	CI[a]	N	SE	Z-Value	P-Value
Intercept	0.73	0.55-0.97	249	0.14	-2.15	0.032
LBP	0.90	0.71-1.13	249	0.12	-0.94	0.348
PRS	1.14	0.73-1.77	249	0.23	0.58	0.564
PRS2	0.88	0.52-1.48	249	0.27	-0.49	0.621
PL	1.08	0.63-1.84	249	0.27	0.28	0.782
Age	1.27	1.01-1.61	249	0.12	2.01	0.045
Age^2	0.66	0.53-0.82	249	0.11	-3.73	<0.001
LBP:Age	0.73	0.58-0.91	249	0.12	-2.80	0.005
LBP:Age^2	1.11	0.87-1.41	249	0.12	0.82	0.415

[a] All betas and confidence intervals (CI) were exponentiated.

^{2} Quadratic age.

Table 1.4. Generalized linear model results comparing annual recruitment success to prior recruitment success for the past year (PRS) and past two years (PRS2), if the prior litter had >1 fawns (PL), and linear and quadratic age. Data obtained from white-tailed deer at the Auburn Captive Facility from 2008 to 2019.

Parameter	Value[a]	CI[a]	N	SE	Z-Value	P-Value
Full Model						
(Intercept)	0.43	0.35-0.53	629	0.10	-8.19	<0.001
PRS	1.42	0.98-2.06	629	0.19	1.86	0.063
PRS2	1.02	0.66-1.56	629	0.22	0.065	0.948
PL	1.02	0.63-1.65	629	0.24	0.092	0.927
Age	1.55	1.28-1.88	629	0.099	4.42	<0.001
Age^2	0.72	0.62-0.84	629	0.078	-4.24	<0.001
Model Excluding PRS2						
(Intercept)	0.43	0.35-0.53	637	0.10	-8.23	<0.001
PRS	1.46	1.03-2.07	637	0.18	2.11	0.035
PL	1.03	0.65-1.63	637	0.24	0.11	0.914
Age	1.55	1.28-1.88	637	0.10	4.52	<0.001
Age^2	0.72	0.62-0.84	637	0.077	-4.22	<0.001

[a] All Betas and confidence intervals were exponentiated.

^{2} Quadratic age.

Table 1.5. Generalized linear model results comparing annual recruitment success to female age groups: Young (0.5-1.5), Prime (2.5-6.5), and Old (7.5-12.5). Data obtained from white-tailed deer at the Auburn Captive Facility from 2008 to 2019.

Parameter	Value[a]	CI[a]	N	SE	Z-Value	P-Value
Young Age Group as Reference						
Intercept	0.18	0.13-0.25	668	0.16	-10.92	<0.001
Age: Young-Old	2.17	1.41-3.32	668	0.22	3.54	<0.001
Age: Young-Prime	2.71	1.94-3.79	668	0.17	5.82	<0.001
Old Age Group as Reference						
Intercept	0.39	0.28-0.55	668	0.17	-5.51	<0.001
Age: Old-Prime	1.25	0.90-1.75	668	0.17	1.31	0.192
Age: Old-Young	0.46	0.30-0.71	668	0.22	-3.54	<0.001

[a] All betas and confidence intervals (CI) were exponentiated.

Table 1.6. Characteristics of female white-tailed deer that were consecutive recruiters compared to non-consecutive recruiting females. And the characteristics of male white-tailed deer that successfully bred with each female group. All data obtained within the Auburn Captive Facility from 2008 to 2019.

Parameter	Consecutive N	Consecutive Avg.	Non-consecutive N[a]	Non-consecutive Avg.	T-Value[b]	P-Value
Female Characteristics						
Longevity	15	9.33	30	4.10	5.19	<0.001
First Recruitment	28[c]	2.29	25	3.20	-2.26	0.030
Last Recruitment	15	7.73	11	3.45	3.87	<0.001
Parasite Load[d]	17	3.51	4	11.29	-1.21	0.305
LBP[e]	24	57.14	9	36.94	1.94	0.076
Male Characteristics						
Sire Age	158	4.99	30	5.97	-1.96[f]	0.049
Sire LBP[e]	153	58.96	26	59.59	-0.11[f]	0.913

[a] Excluded individuals where full life history unknown and unable to determine if consecutively recruited in lifetime.

[b] Welch two sample t-test.

[c] Excluded consecutive recruiters where full reproductive history was unknown.

[d] Average count of ectoparasites present on designated spots of sedated animal.

[e] Lifetime body percentile.

[f] Two sample z-test.

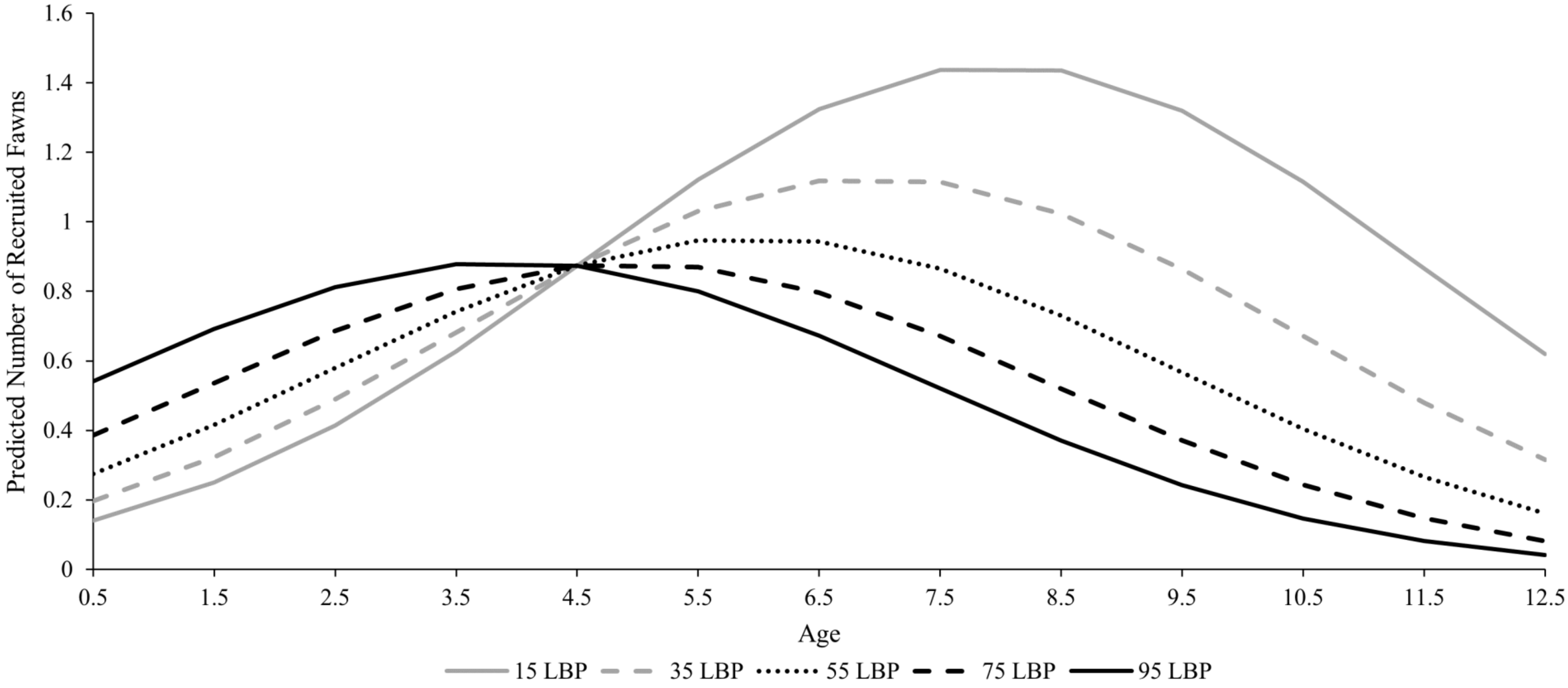

Figure 1.1. Predicted relationship of annual recruitment success of female white-tailed deer in relation to maternal age, at specified lifetime body percentile scores (LBP), based off data at the Auburn Captive Facility from 2008 to 2019. Data were based off a model of 249 breeding season observations of 37 candidate mothers. Recruitment success was based off 260 parentage-known fawns and adjusted to account for a further 49 fawns where parentage was below the 95% confidence threshold.

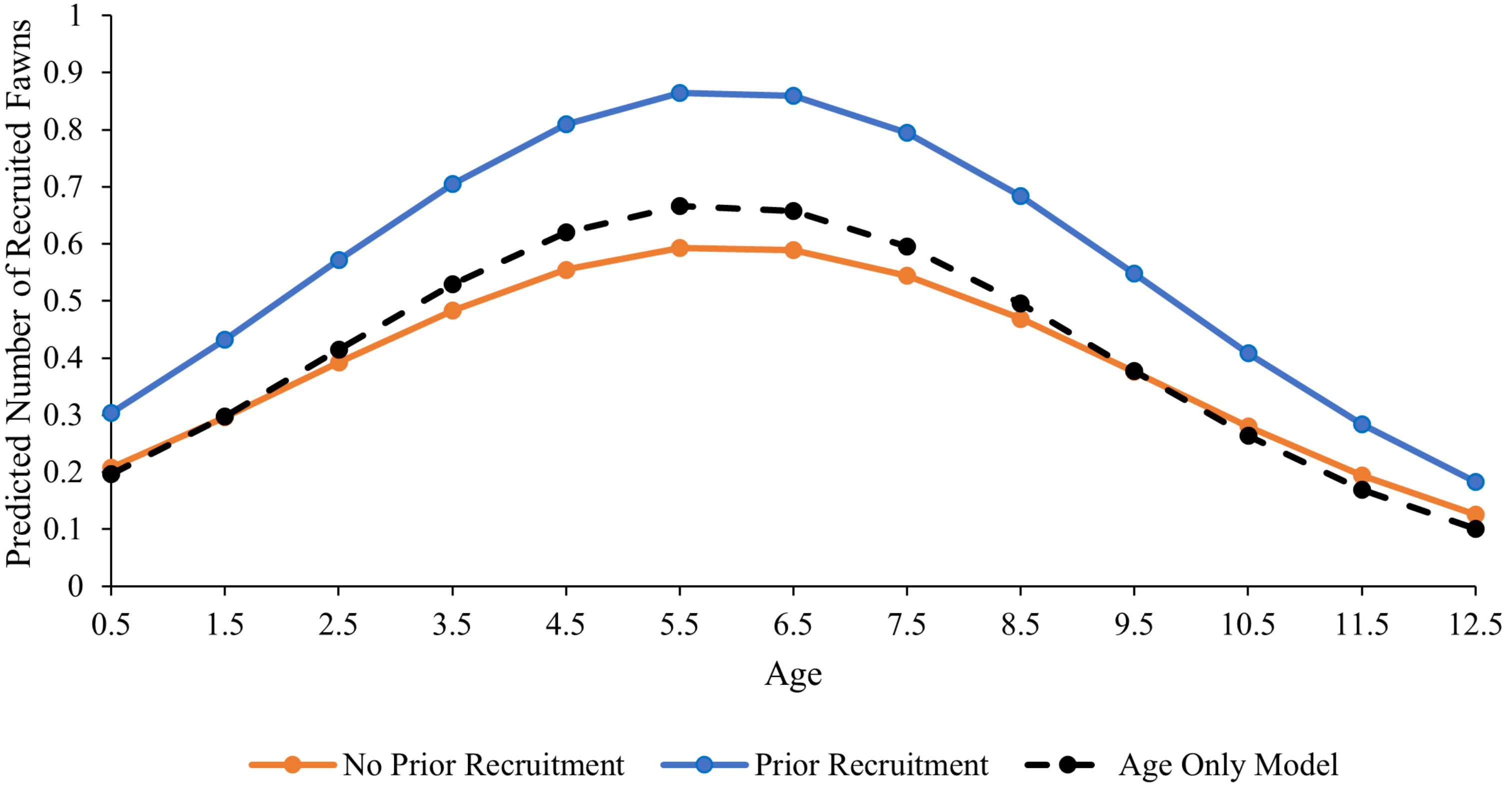

Figure 1.2. Predicted relationship of annual recruitment success of female white-tailed deer in relation to maternal age and prior year's reproductive history based off data at the Auburn Captive Facility from 2008 to 2019. Curves were based off two models, one to account for Age and PRS with 637 breeding season observations of 151 candidate mothers (Blue and Orange) and one to account for only age with 668 breeding season observations of 156 individuals. For both models, recruitment success was based off 260 parentage-known fawns and adjusted to account for a further 49 fawns where parentage was below the 95% confidence threshold.

Chapter 2: Phenotypic characteristics of successful mated pairs in white-tailed deer (*Odocoileus virginianus*): Evidence of positive assortative mating.

Abstract

Based on principles of natural selection, high-quality individuals should select mates of similar phenotypic quality when given the opportunity; this follows the idea of positive assortative mating. In ungulates, the idea of mate selectivity is still highly debated, with few studies yet able to document direct evidence of positive assortative mating. In white-tailed deer (*Odocoileus virginianus*), recent studies have suggested that mating is random, with minimal selectivity by individuals. However, it is unclear if these findings are because study populations are still undergoing demographic changes (e.g., age structure and sex ratio) that may not present opportunities for preferential mating. From 2008 to 2019 we studied a captive population of white-tailed deer to examine characteristics of 184 mated pairs that successfully recruited fawns, while the population underwent changes in age structure and sex ratio. We found verification of positive assortative mating in mated pairs. Specifically, for each 1-year increase in female age there was a 0.17-year increase in male age ($P = 0.002$) among mated pairs, and for every 1.00 cm increase in female skeletal body size there was a 0.44 cm increase in male skeletal body size ($P = 0.006$). Furthermore, we observed no random mating within the population while also documenting a decrease in younger males breeding as the age structure matured. However, we still observed cases where there was a large difference in age between mates, indicating some plasticity with mating. Our results suggest that high-quality individuals will select individuals of a similar quality if provided the opportunity. However, choosiness appears dynamic, with a decrease in selectivity when preferential mates are limited due to young age structure or when mating opportunities decrease for poor competitors in a mature age structure.

Keywords

assortative mating, breeding systems, mated pairs, microsatellites, *Odocoileus virginianus*, recruitment, white-tailed deer

Introduction

Theories on sexual selection in mammals primarily state that mating systems are guided by females selecting males based off sexually selected traits that maximize offspring fitness (Darwin 1874; Fishers 1930; Trivers 1972). Following this, it is generally believed that older, socially dominant males of a larger body size, and elaborate ornamentation often have the greatest reproductive success because these characteristics are positively correlated with high fitness and provide an advantage in intrasexual competition (Darwin 1871; Zahavi 1975; Emlen and Oring 1977; Clutton-Brock 1989). This is especially true in ungulates, where mating systems are generally polygynous and there is pronounced sexual dimorphism (Jarman 1983). It is generally believed that most, if not all, sexually mature females in a population are bred by a few dominant males (Alexander et al. 1979; Clutton-Brock 1989). While female ungulates are expected to be the choosier sex because of greater parental investment (Emlen and Oring 1977; Johnstone et al. 1996), both sexes may select for certain qualities when choosing mates (Zahavi 1975; Dewsbury 1982; Andersson 1994; Jennions and Petrie 1997).

There is considerable debate amongst scientists whether female mate choice in ungulates is driven by intrasexual competition, male coercion, or individuals undergoing active choice (Clutton-Brock and McAuliffe 2009). However, an increasing number of studies in ungulates are suggesting that males may be choosier when selecting potential mates than previously thought (Berger 1989; Preston et al. 2005), further complicating the current understanding of mate selectivity in polygynous ungulates. For decades our understanding of mating systems in ungulates was largely based off studies of polygynous species in open landscapes (Murie 1951; Bergerud 1974; Clutton-Brock et al. 1982; Byers 1997; Wolff 1998). While these studies were greatly informative, they were generally limited to harem breeding species and not necessarily reflective of breeding patterns and mate selectivity in ungulates inhabiting more forested landscapes. As a result, breeding systems and mate selection strategies for cryptic species such as white-tailed deer (*Odocoileus virginianus*) were poorly understood (Bowyer et al. 2020). For example, Hirth (1977) was only able to observe 4 confirmed copulations over a 2-year span, in what was considered for years to be the seminal work on reproductive patterns in the species.

More recently, new tools and technologies have enabled us to better understand the mating systems of white-tailed deer. Studies using genetic techniques have revealed that monopolization by males is less common than expected, and males from multiple age classes successfully breed females (Sorin 2004; DeYoung et al. 2009). However, our understanding of the phenotypic characteristics of mated pairs is still poorly understood. Theory postulates that positive assortative mating (Burley 1983) should occur in a population where high-quality individuals are present, often resulting in high-quality individuals selecting for mates of a similar quality (Fawcett and Johnstone 2003). In white-tailed deer, Neuman et al. (2016) examined age and body size relationships of mated pairs using microsatellite analysis. They observed high plasticity in mating success regarding age and body size relationships, indicating random mating was occurring within the population with no evidence of positive assortative mating (Neuman et al. 2016). However, they believed this may have been observed due to a changing herd demographic during the study where the young male age structure and female skewed sex ratio allowed for increased breeding opportunity for males of varying sizes and ages (Neuman et al. 2016). This begs the question if preferential mating by high-quality individuals (e.g., older, large body size) occurs at a lesser frequency when the probability of finding a mate of similar phenotypic quality is poor.

In this study, we examined mate selection and its influence on recruitment success in a captive population of white-tailed deer allowed to breed naturally. Our goal was to improve understanding of the characteristics of mated pairs that successfully recruited fawns. This study utilized the same population and incorporated some of the data as Neuman et al. (2016). Our specific objective was to evaluate age and body size characteristics of mated pairs within the population now that the male age structure was older and the sex ratio balanced. We hypothesized that we would find no evidence of random mating within the population and instead find evidence of positive assortative mating for age and body size in mated pairs.

Material and Methods

Study Area

This study examined a captive population of white-tailed deer at the Auburn Captive Facility (ACF) located 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 land cover types within the facility consisted primarily of actively managed hay fields (40%) and mixed forests (60%). The primary tree species within ACF included oak (*Quercus* spp.), sweetgum (*Liquidambar styraciflua*), hickory (*Carya* spp.), and loblolly pine (*Pinus taeda*) with naturally regenerated understory thickets of blackberry (*Rubus* spp.), eastern red cedar (*Juniperus virginiana*), and Chinese privet (*Ligustrum sinense*). Prescribed fire was conducted sparsely throughout the property where applicable. The predominant grass species within ACF was Bermuda grass (*Cynodon dactlyon*), but fescue (*Festuca* sp.), big bluestem (*Andropogon gerardi*), Johnson grass (*Sorghum halepense*), dallisgrass (*Paspalum dilatatum*), and bahia grass (*P. notatum*) were also present. 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 at 137 cm based off data from the nearest National Oceanic and Atmospheric Administration weather station (NOAA National Centers for Environmental information 2022). Elevation within the facility ranged from 190–225 m above sea level. 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 three timed feeders (Newbolt et al. 2017).

Capture Techniques

Deer were captured mid-September to mid-March annually from 2008 through 2019 using two techniques. From 2008 through 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 in one trapping effort and is further described by Neuman et al. (2016). Beginning in 2014, all deer were immobilized and captured only by darting. The dart guns fired telemetry darts using .22 caliber blanks and were fitted with night vision scopes (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 125mg/ml and given at a rate of 2.2mg/kg) and Xylazine® (at a concentration of 100mg/ml given at a rate of 2.2mg/kg) (Kilpatrick et al. 1996). To ensure minimal chance of capture related mortality, deer were not darted until at least 6 months of age. If a fawn was captured and later determined to not have survived to recruitment age (6 months) it was excluded from further analysis due to our research objectives pertaining to mated pairs that successfully recruited fawns. Darters sat in elevated tree stands overlooking the feeders, previously mentioned, 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 to reverse sedation (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. This was due to the high accuracy of this technique with these age classes (Gee et al. 2002). Three skeletal body size measurements were conducted using a flexible measuring tape. The measurements were body length (tip of the snout to the proximal end of the tail, following a straight line along the backbone), chest girth (circumference of the chest directly posterior of front legs), and hind foot length (measured from the tip of the hoof to the posterior end of the tuber calcis; Neuman et al. 2016). 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-cm^2 piece of tissue. Samples were placed in a Cryule plastic cryogenic vial (Wheaton, Millville, NJ), properly labeled for identification, and then placed in a

-80° C freezer for preservation 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).

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, allelic richness (El Mousadik and Petit 1996), gene diversity (Nei 1987), and the inbreeding coefficient (Weir and Cockerham 1984). We detected significant departures from Hardy-Weinberg equilibrium at 2 of the 18 loci (Table 2.1); however, these loci were still included in our parentage assignment analysis due to 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 for a year if they were visually observed or detected during annual camera surveys. Fawns were added to 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 removed from a candidate parent list and presumed deceased if not detected on camera or observed for two years.

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 of 0.074, and an assumption that 90% of the population in ACF was 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 confidence level was 95%, similar to methods used in prior studies at ACF (Neuman et al. 2016, Newbolt et al. 2017, Gomes 2020, Ivy-Israel et al. 2020).

Statistical Analysis

We used three skeletal measurements (hind foot, body length, and chest girth) to represent body size and skeletal growth of an individual (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). Due to our inability to obtain measurements every year of an individual’s life, we created lifetime values to account for this. First, we used Welch two sample t-tests and two sampled z-tests to compare average body size between age groups for each sex. This allowed us to determine when cessation of skeletal growth occurred in each sex. In females, we detected no significant difference in body size between 3.5 and 4.5 years of age ($P = 0.349$), and there was no significant difference for males between 5.5 and 6.5 years of age ($P = 0.891$; Table 2.2). Based off these findings, we determined that maximized skeletal growth occurred by 3.5 years of age in females and 5.5 years of age in males, similar to Ditchkoff et al. (1997).

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 they had at least one maximized body size measurement collected, we used that measurement for the year they were known to have successfully mated. For example, if it was determined a female was bred at 8.5 years of age but a measurement hadn’t been obtained since 5.5 years of age, we used that body size measurement since maximized skeletal growth occurs in females at 3.5 years. We also calculated a lifetime body percentile (LBP) and used this statistic as a surrogate for skeletal body size, similar to Neuman et al. (2016). 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). 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. Using these measurements, we examined three separate relationships of mated pairs: when body size measurements were collected within a year of the breeding event, when individuals had body size measurements collected within the last year and including any maximized body size measurements, and when both individuals had a lifetime body percentile. All linear regression analyses for body size (package stats) were conducted in the software program R (version 4.0.2; R Core Development Team 2022).

Using a chi-squared test, we compared the difference in age between individuals in mated pairs to the expected age difference between mated pairs assuming random mating within the population. Expected age differences were based off our annual candidate parent lists where we examined all possible annual combinations from 2008 to 2019 in ACF. We examined age relationships using linear regression in the software program R. Furthermore, for age relationships we divided mated pairs into three categories: “Both Young Adults”, “One Young Adult”, and “Two Mature Adults”, to examine the proportion of each grouping observed in a breeding season over time. Using our findings for maximized skeletal size, we considered mature adults to be any female ≥3.5 years of age and any males ≥5.5 years of age. We examined this relationship using linear regression in the software program R. To compare between groups in cases of multiple paternity (e.g., litters >1 with more than one sire) we used a Welch two sample t-test in the software program R. Furthermore, when examining the annual frequency of multiple paternity events, we used a Fisher’s exact 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.

Results

Based off annual camera surveys and capture and mortality records, we determined that the population of ACF ranged annually from 71 to 139 individuals from 2008 to 2019 (Table 2.3). Generally, population density (including recruited fawns) increased from the beginning of the study until 2017, and the adult sex ratio was approximately equal throughout the course of the study. The male age structure matured during the course of the study: average age of candidate sires (including male fawns) in 2008 was 1.42 years (SE = 0.20; N = 25) and peaked in 2018 at 4.38 years (SE = 0.40; N = 60; Figure 2.1). Similarly, the female age structure matured from 2.15 years of age (SE = 0.24; N = 46) in 2008 and peaked at 6.79 years (SE = 0.53; N = 42) in 2019. The proportion of breeding events where a male ≤3.5 years of age sired a fawn decreased over time as the proportion of males ≥4.5 years of age increased in the population

(Figure 2.2), with no documentation of sires ≤3.5 years of age in 2019 (Figure 2.3). We documented 383 recruited fawns during the study, and 309 were of known age. We were able to identify both parents at the 95% confidence level for 211 of these fawns, and they came from 184 litters.

The distribution of age differences between mated pairs was significantly different (χ^2 = 59.36; d.f. = 25; $P < 0.001$; Figure 2.4) than the distribution of age differences from a random assortment of mates. We found that cases where the male was 3 to 4 years older than the female had the greatest difference in observed frequency compared to the expected frequency. Our largest observed age difference was 9 years where a 9.5-year-old female bred with a male fawn. Our oldest female and male to successfully breed were 12.5 and 11.5 years old, respectively. We observed 16 mated 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, we found a significant linear relationship where for every 1-year increase in female age we saw a 0.17-year increase in male age ($t = 3.08$, d.f. = 182, $P = 0.002$; Figure 2.5). As the age structure matured for both sexes, we observed an increase over time in the proportion of mature mated pairs. For every 1-year progression in the study the proportion of mature mated pairs increased by 7.77% ($t = 7.0$, d.f. = 10, $P < 0.001$), while pairings where both adults were young decreased by 4.30% ($t = -5.18$, d.f. = 10, $P < 0.001$; Figure 2.6).

We observed no significant linear relationship between lifetime body percentiles of 108 mated pairs ($t = 1.12$, d.f. = 106, $P = 0.267$; Figure 2.7). Furthermore, using skeletal body size measurements, we observed no significant linear relationship for body size when examining 24 mated pairs where body size measurements were collected for both parents that year ($t = 1.08$, d.f. = 22, $P = 0.292$; Figure 2.8). We had 83 confirmed mated pairs with body size measurements for both sexes when we accepted body size from that year, the previous year, or the animal was mature and we had a maximized body measurement. In this subset of our data, we found a positive relationship where male skeletal body size increased by 0.44 cm for every 1.00 cm increase in female skeletal body size (t = 2.81, d.f. = 81, P = 0.006; Figure 2.9).

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 our 12 multiple paternity events, 10 (83.3%) occurred in 2013 or before (Figure 2.10). However, using a Fisher's exact test we found no significance (P = 0.158) between the frequency of multiple paternity events and whether it was early or late in the study. The average age of females in non-multiple paternity events 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 Welch two sample t-test we found no significant difference in age between groups (t = -1.11, P = 0.282). 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 Welch two sample t-test we found a significant difference in age between groups (t = 2.07, P = 0.044). The average age difference between a female and males during a multiple paternity event was 2.21 years of age (SE = 0.34, N = 24), and in 75% of cases 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 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; using a Welch two sample t-test we found no significant difference in body size between groups (t = 0.90, P = 0.384). The average body 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 Welch two sample t-test we found no significant difference in body size between groups (t = -1.06, P = 0.299). 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 Welch two sample t-test we found no significant difference in the body size difference of mated pairs between groups (t = -0.21, P = 0.834). 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 original hypothesis, we found evidence of positive assortative mating based on age in mated pairs. Evidence of age-based assortative mating in ungulates is limited, but has been observed in bison (*Bison bison*; Wolff 1988) and fallow deer (*Dama dama*; Farrell et al. 2011). We believe these findings indicate age may be an indicator of quality and speculate that high-quality individuals are selecting for other individuals of a similar quality (Fawcett and Johnstone 2003). In the current literature on ungulates, fitness is often found to improve with increasing age in both males and females (Clutton-Brock et al. 1982; Byers 1997; Weladji et al. 2006; Vanpé et al. 2009*b*; Festa-Bianchet 2012) and evidence from our study population also supports this (Newbolt et al. 2017; see Chapter 1). 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; Willisch et al. 2012; Morina et al. 2018). Furthermore, we observed a decrease over time in the annual proportion of breeding events involving males ≤3.5 years of age. It is well documented in ungulates that as male age structure matures and the sex ratio becomes balanced, fewer males are able to participate in breeding (Bergerud 1974; Clutton-Brock et al. 1997; Røed et al. 2002; Mysterud et al. 2004; Markussen et al. 2019). As our study progressed and more mature males were present, competition for mating likely increased, making it more difficult for immature males to actively participate in courtship rituals without conspecific competition (Ozoga and Verme 1985). As mature adults selected for similar mates, young adults may have selected for other young adults due to fewer breeding opportunities available for each sex, similar to the findings of Farrell et al. (2011). 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 off the perception of age is still obscure in ungulates, but recent evidence in mountain goats (*Oreamnos americanus*) suggests maternal experience may be a good indicator of fitness in females and have a positive influence on male mate preference (Mainguy et al. 2008).

We found no evidence of random age-based mating within the population. This is contrary to Neuman et al. (2016) findings at ACF. However, they speculated that they may have observed random mating in their analysis 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 in an area: if availability is low then choosiness should decrease (Real 1990; Jennions and Petrie 1997). We observed an increase in mature pairings as the age structure increased for both sexes. Under a young male age structure, females may have fewer preferred males to choose from, and mate selectivity with regards to age should 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 strategy by female white-tailed deer when potential mate quality is suboptimal.

In support of our hypothesis, we found that there was positive assortative mating for skeletal body size. Assortative mating based off physical features has largely been observed in arthropods (Brown 1990; Jiang et al. 2013) and birds (Bortolotti and Iko 1992; Delestrade 2001; Jawor et al. 2003). However, in reindeer and soay sheep (*Ovis aries*) it has been found that individuals 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 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). Evidence that males select mates based on female 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 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 there exists a situational tradeoff 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, they should be choosy (Johnstone 1997). Similarly, as the population size and age structure increased at ACF we speculate that selectivity likely increased due to a greater availability of preferential mates.

Despite the lack of evidence for random mating in our population, we still observed cases of significant differences in age and body size of mated pairs, further documenting plasticity with mating within the population. This also provides further evidence 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), contrary to other polygynous ungulate mating systems (Clutton-Brock et al. 1982; Clutton-Brock et al. 1992; 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 mated 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 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). These lesser quality 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 that sired the fawns. Multiple copulations or multiple paternity have been observed in a variety of ungulates (Endo and Doi 2002; Carling et al. 2003; Briefer et al. 2013; Vanpé et al. 2009*a*; Coombs et al. 2022) including white-tailed deer (DeYoung et al. 2002; Sorin 2004; DeYoung et al. 2006), but the debate in the literature is still ongoing why this phenomenon occurs (Wolff and Macdonald 2004). 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. We observed an average age difference of 2 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.

Literature Cited

Airst J.I., Lingle S. 2019. Courtship strategies of white-tailed deer and mule deer males when living in sympatry. Behaviour 156:307–330.

Airst J.I., Lingle S. 2020. Male size and alternative mating tactics in white-tailed deer and mule deer. Journal of Mammalogy 101:1231–1243.

Alexander R.D., Hoogland J.L., Howard R.D., Noonan K.M., Sherman P.W. 1979. Sexual dimorphisms and breeding systems in pinnipeds, ungulates, primates, and humans. In: Evolutionary biology and human social behavior: An anthropological perspective. Duxbury Press, North Scituate, Massachusetts; p. 402–435.

Anderson J.D., Honeycutt R.L., Gonzales R.A., Gee K.L., Skow L.C., Gallagher R.L., Honeycutt D.A., DeYoung R.W. 2002. Development of microsatellite DNA markers for the automated genetic characterization of white-tailed deer populations. Journal of Wildlife Management 66:67–74.

Andersson M. 1994. Sexual selection. Princeton University Press, Princeton, New Jersey.

Asa C.S. 1999. Male reproductive success in free-ranging feral horses. Behavioral Ecology and Sociobiology 47:89–93.

Bartareau T.M. 2019. Estimating body mass of Florida white-tailed deer from standard age and morphometric measurements. Wildlife Research 46:334–342.

Berger J. 1989. Female reproductive potential and its apparent evaluation by male mammals. Journal of Mammalogy 70:347–358.

Bergerud A.T. 1974. Rutting behaviour of Newfoundland caribou. In: Geist V., Walther F., editors. The behaviour of ungulates and its relation to management, Volume 1. IUCN, Morges, Switzerland; 395–435.

Bortolotti G.R., Iko W.M. 1992. Non-random pairing in American kestrels: mate choice versus intra-sexual competition. Animal Behaviour 44:811–821.

Bowyer R.T., Bleich V.C., Manteca X., Whiting J.C., Stewart K.M. 2007. Sociality, mate choice, and timing of mating in American bison (*Bison bison*): effects of large males. Ethology 113:1048–1060.

Bowyer R.T., McCullough D.R., Rachlow J.L., Ciuti S., Whiting J.C. 2020. Evolution of ungulate mating systems: Integrating social and environmental factors. Ecology and Evolution 10:5160–5178.

Briefer E.F., Farrell M.E., Hayden T.J., McElligott A.G. 2013. Fallow deer polyandry is related to fertilization insurance. Behavioral Ecology and Sociobiology 67:657–665.

Brown W.D. 1990. Size-assortative mating in the blister beetle *Lytta magister* (Coleoptera: Meloidae) is due to male and female preference for larger mates. Animal Behaviour 40:901–909.

Burley N. 1983. The meaning of assortative mating. Ethology and Sociobiology 4:191–203.

Byers J.A. 1997. American pronghorn: social adaptations and the ghosts of predators past. University of Chicago Press, Chicago, Illinois.

Byers J.A., Moodie J.D., Hall N. 1994. Pronghorn females choose vigorous mates. Animal Behaviour 47:33–43.

Byers J.A., Waits L. 2006. Good genes sexual selection in nature. Proceedings of the National Academy of Sciences 103:16343–16345.

Carling M.D., Wiseman P.A., Byers J.A. 2003. Microsatellite analysis reveals multiple paternity in a population of wild pronghorn antelopes (*Antilocapra americana*). Journal of Mammalogy 84:1237–1243.

Ceacero F., García A.J., Landete-Castillejos T., Bartošová J., Bartoš L., Gallego L. 2012. Benefits for dominant red deer hinds under a competitive feeding system: food access behavior, diet and nutrient selection. Plos one 7:e32780.

Charlton B.D., Reby D., McComb K. 2007. Female red deer prefer the roars of larger males. Biology Letters 3:382–385.

Clutton-Brock T.H. 1989. Review lecture: mammalian mating systems. Proceedings of the Royal Society of London. B. Biological Sciences 236:339–372.

Clutton-Brock T.H., Albon S.D., Guinness F.E. 1989. Fitness costs of gestation and lactation in wild mammals. Nature 337:260–262.

Clutton-Brock T.H., Guinness F.E., Albon S.D. 1982. Red deer: behavior and ecology of two sexes. University of Chicago Press, Chicago, Illinois.

Clutton-Brock T., McAuliffe B.K. 2009. Female mate choice in mammals. The Quarterly review of biology 84:3–27.

Clutton-Brock T.H., Price O.F., MacColl A.C. 1992. Mate retention, harassment, and the evolution of ungulate leks. Behavioral Ecology 3:234–242.

Clutton-Brock T.H., Rose K.E., Guinness F.E. 1997. Density–related changes in sexual selection in red deer. Proceedings of the Royal Society of London. Series B: Biological Sciences 264:1509–1516.

Coltman D.W., Festa-Bianchet M., Jorgenson J.T., Strobeck C. 2002. Age-dependent sexual selection in bighorn rams. Proceedings of the Royal Society of London. Series B: Biological Sciences 269:165–172.

Coombs K.R., Weladji R.B., Holand Ø., Røed K.H. 2022. Mismatch between calf paternity and observed copulations between male and female reindeer: Multiple mating in a polygynous ungulate?. Current Zoology 2022:zoac054.

Côté S.D., Festa-Bianchet M. 2001. Reproductive success in female mountain goats: the influence of age and social rank. Animal Behaviour 62:173–181.

Dakin E.E., and J.C. Avise. 2004. Microsatellite null alleles in parentage analysis. Heredity 93:504–509.

Darwin C. 1871. The descent of man, and selection in relation sex. John Murray, London, United Kingdom.

Darwin C. 1874. The descent of man and selection in relation to sex. Volume 2. John Murray, London, United Kingdom.

Delestrade A. 2001. Sexual size dimorphism and positive assortative mating in Alpine Choughs (*Pyrrhocorax graculus*). The Auk 118:553–556.

Dewsbury D.A. 1982. Ejaculate cost and male choice. The American Naturalist 119:601–610.

DeYoung R.W., and K.V. Miller. 2011. White-tailed deer behavior. In: Hewitt D.G., editor. Biology and management of white-tailed deer. CRC Press, Boca Raton, Florida; p. 311–351.

DeYoung R.W., Demarais S., Gee K.L., Honeycutt R.L., Hellickson M.W., Gonzales R.A. 2009. Molecular evaluation of the white-tailed deer (*Odocoileus virginianus*) mating system. Journal of Mammalogy 90:946–953.

DeYoung R.W., Demarais S., Gonzales R.A., Honeycutt R.L., Gee K.L. 2002. Multiple paternity in white-tailed deer (*Odocoileus virginianus*) revealed by DNA microsatellites. Journal of Mammalogy 83:884–892.

DeYoung R.W., Demarais S., Honeycutt R.L., Gee K.L., Gonzales R.A. 2006. Social dominance and male breeding success in captive white-tailed deer. Wildlife Society Bulletin 34:131–136.

Ditchkoff S.S., Lochmiller R.L., Masters R.E., Starry W.R., Leslie Jr D.M. 2001. Does fluctuating asymmetry of antlers in white–tailed deer (*Odocoileus virginianus*) follow patterns predicted for sexually selected traits?. Proceedings of the Royal Society of London. Series B: Biological Sciences 268:891–898.

Ditchkoff S.S., Welch Jr E.R., Starry W.R., Dinkines W.C., Masters R.E., Lochmiller R.L. 1997. Quality deer management at the McAlester Army Ammunition Plant: a unique approach. Proceedings of the annual conference of the Southeastern Association of Fish and Wildlife Agencies 51:389–399.

El Mousadik A., and R. J. Petit. 1996. High level of genetic differentiation for allelic richness among populations of the argan tree [*Argania spinosa* (L.) Skeels] endemic to Morocco. Theoretical and Applied Genetics 92:832–839.

Emlen S.T., and L.W. Oring. 1977. Ecology, sexual selection, and evolution of mating systems. Science 197:215–223.

Endo A., and Doi T. 2002. Multiple copulations and post-copulatory guarding in a free-living population of sika deer (*Cervus nippon*). Ethology 108:739–747.

Farrell M.E., Briefer E., McElligott A.G. 2011. Assortative mating in fallow deer reduces the strength of sexual selection. PLoS One 6:e18533.

Fawcett T.W., Johnstone R.A. 2003. Mate choice in the face of costly competition. Behavioral Ecology 14:771–779.

Festa-Bianchet M. 2012. The cost of trying: weak interspecific correlations among life-history components in male ungulates. Canadian Journal of Zoology 90:1072–1085.

Fisher R.A. 1930. The Genetical Theory of Natural Selection. Clarendon Press, Oxford, United Kingdom.

Flajšman K., Jerina K., Pokorny B. 2017. Age-related effects of body mass on fertility and litter size in roe deer. PloS one 12:e0175579.

Gee K.L., Holman J.H., Causey M.K., Rossi A.N., Armstrong J.B. 2002. Aging white-tailed deer by tooth replacement and wear: a critical evaluation of a time-honored technique. Wildlife Society Bulletin 30:387–393.

Geist V. 1982. Adaptive behavior strategies. In: Thomas J.W., Toweill D.E., editors. Elk of North America. Stackpole Books, Harrisburg, Pennsylvania; p. 219–277.

Gomes M. Patterns of Testosterone in White-tailed Deer and their Relationship to Reproductive Success. Master's Thesis, Auburn University, Auburn, Alabama.

Haugen A.O. 1959. Breeding records of captive white-tailed deer in Alabama. Journal of Mammalogy 40:108–113.

Hirth D.H. 1977. Social behavior of white-tailed deer in relation to habitat. Wildlife Monographs 53:1–55.

Huang K. 2018. Parentage V1.1 Manual. Northwest University, Xi'an, China. https://github.com/huangkang1987/parentage/raw/master/parentage_1.1d.zip

Huang K., Mi R., Dunn D.W., Wang T., Li B. 2018. Performing parentage analysis in the presence of inbreeding and null alleles. Genetics 210:1467–1481.

Ivy-Israel N., Moore C.E., Schwartz T.S., Ditchkoff S.S. 2020. Characterization of two MHC II genes (DOB, DRB) in white-tailed deer (*Odocoileus virginianus*). BMC genetics 21:1–7.

Jarman P. 1983. Mating system and sexual dimorphism in large terrestrial, mammalian herbivores. Biological Reviews 58:485–520.

Jawor J.M., Linville S.U., Beall S.M., Breitwisch R. 2003. Assortative mating by multiple ornaments in northern cardinals (*Cardinalis cardinalis*). Behavioral Ecology 14:515–520.

Jennions M.D., and M. Petrie. 1997. Variation in mate choice and mating preferences: a review of causes and consequences. Biological Reviews 72:283–327.

Jiang Y., Bolnick D.I., Kirkpatrick M. 2013. Assortative mating in animals. The American Naturalist 181:E125-138.

Johnstone R.A. 1997. The tactics of mutual mate choice and competitive search. Behavioral Ecology and Sociobiology 40:51–59.

Johnstone R.A., Reynolds J.D., Deutsch J.C. 1996. Mutual mate choice and sex differences in choosiness. Evolution 50:1382–1391.

Jones A.G., and W.R. Arden. 2003. Methods of parentage analysis in natural populations. Molecular Ecology 12:2511–2523.

Jones P.D., Strickland B.K., Demarais S., DeYoung R.W. 2011. Inconsistent association of male body mass with breeding success in captive white-tailed deer. Journal of Mammalogy 92:527–533.

Karns G.R., Holland A.M., Steury T.D., Ditchkoff S.S. 2014. Maternal life history of white-tailed deer: factors affecting fetal sex allocation, conception timing, and senescence. Evolutionary Ecology Research 16:165–178.

Kie J.G., Johnson B.K., Noyes J.H., Williams C.L., Dick B.L., Rhodes O.E., Stussy R.J., Bowyer R.T. 2013. Reproduction in North American elk Cervus elaphus: paternity of calves sired by males of mixed age classes. Wildlife Biology 19:302–310.

Kilpatrick H. J., DeNicola A.J., Ellingwood M.R. 1996. Comparison of standard and transmitter-equipped darts for capturing white-tailed deer. Wildlife Society Bulletin 24:306–331.

Komers P.E., Birgersson B., Ekvall K. 1999. Timing of estrus in fallow deer is adjusted to the age of available mates. The American Naturalist 153:431–436.

Langbein J., Thirgood S.J. 1989. Variation in mating systems of fallow deer (*Dama dama*) in relation to ecology. Ethology 83:195–214.

Le Boeuf B., Condit R., Reiter J. 2019. Lifetime reproductive success of northern elephant seals (*Mirounga angustirostris*). Canadian Journal of Zoology 97:1203–1217.

Lemasson A., Remeuf K., Trabalon M., Cuir F., Hausberger M. 2015. Mares prefer the voices of highly fertile stallions. PLoS One 10:e0118468.

Mainguy J., Côté S.D., Cardinal E., Houle M. 2008. Mating tactics and mate choice in relation to age and social rank in male mountain goats. Journal of Mammalogy 89:626–635.

Markussen S.S., Herfindal I., Loison A., Solberg E.J., Haanes H., Røed K.H., Heim M., Sæther B.E. 2019. Determinants of age at first reproduction and lifetime breeding success revealed by full paternity assignment in a male ungulate. Oikos 128:328–337.

Martin A.M., Festa-Bianchet M., Coltman D.W., Pelletier F. 2016. Demographic drivers of age-dependent sexual selection. Journal of Evolutionary Biology 29:1437–1446.

McElligott A.G., Gammell M.P., Harty H.C., Paini D.R., Murphy D.T., Walsh J.T., Hayden T.J. 2001. Sexual size dimorphism in fallow deer (*Dama dama*): do larger, heavier males gain greater mating success?. Behavioral Ecology and Sociobiology 49:266–272.

Miller B.F., Muller L.I., Doherty T., Osborn D.A., Miller K.V., Warren R.J. 2004. Effectiveness of antagonists for tiletamine-zolazepam/xylazine immobilization in female white-tailed deer. Journal of Wildlife Diseases 40:533–537.

Miller B.F., Muller L.I., Storms T.N., Ramsay E.C., Osborn D.A., Warren R.J., Miller K.V., Adams K.A. 2003. A comparison of carfentanil/xylazine and Telazol®/xylazine for immobilization of white-tailed deer. Journal of Wildlife Diseases 39:851–858.

Monteith K.L., Bleich V.C., Stephenson T.R., Pierce B.M., Conner M.M., Kie J.G., Bowyer R.T. 2014. Life-history characteristics of mule deer: effects of nutrition in a variable environment. Wildlife Monographs 186:1–62.

Morina D.L., Demarais S., Strickland B.K., Larson J.E. 2018. While males fight, females choose: male phenotypic quality informs female mate choice in mammals. Animal Behaviour 138:69–74.

Murie O.J. 1951. The elk of North America. Stackpole Books, Harrisburg, Pennsylvania.

Mysterud A., Langvatn R., Stenseth N.C. 2004. Patterns of reproductive effort in male ungulates. Journal of Zoology 264:209–215.

Nei M. 1987. Molecular evolutionary genetics. Columbia University Press, New York, New York.

Neuman T.J., Newbolt C.H., Ditchkoff S.S., Steury T.D. 2016. Microsatellites reveal plasticity in reproductive success of white-tailed deer. Journal of Mammalogy 97:1441–1450.

Newbolt C.H., Acker P.K., Neuman T.J., Hoffman S.I., Ditchkoff S.S., Steury T.D. 2017. Factors influencing reproductive success in male white-tailed deer. The Journal of Wildlife Management 81:206–217.

Nixon C.M. 1971. Productivity of white-tailed deer in Ohio. The Ohio Journal of Science 71:217–225.

NOAA National Centers for Environmental information [NCEI]. 2022. Climate at a Glance. April 2022. https://www.ncei.noaa.gov/. Accessed April 2022.

Ozoga J. J., and L. J. Verme. 1985. Comparative breeding-behavior and performance of yearling vs prime-age white-tailed bucks. Journal of Wildlife Management 49:364–372.

Pero E.M., Chitwood M.C., Hildreth A.M., Berkman L.K., Keller B.J., Sumners J.A., Hansen L.P., Isabelle J.L., Eggert L.S., Titus C.L., Millspaugh J.J. 2021. Acclimation of elk mating system following restoration to the Missouri Ozarks, USA. Restoration Ecology 30:e13623.

Preston B.T., Stevenson I.R., Pemberton J.M., Coltman D.W., Wilson K. 2005. Male mate choice influences female promiscuity in Soay sheep. Proceedings of the Royal Society B: Biological Sciences 272:365–373.

R Development Core Team. 2014. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/

Real L. 1990. Search theory and mate choice. I. Models of single-sex discrimination. The American Naturalist 136:376–405.

Rhodes Jr O.E., Novak J.M., Smith M.H., Johns P.E. 1986. Assessment of fawn breeding in a South Carolina deer herd. Proceedings of the annual conference of the Southeastern Association of Fish and Wildlife Agencies 40:430–437.

Robinson M.R., Pilkington J.G., Clutton-Brock T.H., Pemberton J.M., Kruuk L.E. 2006. Live fast, die young: trade-offs between fitness components and sexually antagonistic selection on weaponry in Soay sheep. Evolution 60:2168–2181.

Roseberry J.L., Klimstra W.D. 1975. Some morphological characteristics of the Crab Orchard deer herd. The Journal of Wildlife Management 39:48–58.

Røed K.H., Holand Ø., Smith M.E., Gjøstein H., Kumpula J., Nieminen M. 2002. Reproductive success in reindeer males in a herd with varying sex ratio. Molecular Ecology 11:1239–1243.

Schultz S.R., and M.K. Johnson. 1992. Breeding by male white-tailed deer fawns. Journal of Mammalogy 73:148–150.

Severinghaus C. W. 1949. Tooth development and wear as criteria of age in white-tailed deer. Journal of Wildlife Management 13:195–216.

Shabihkhani M., Lucey G.M., Wei B., Mareninov S., Lou J.J., Vinters H.V., Singer E.J., Cloughesy T.F., Yong W.H. 2014. The procurement, storage, and quality assurance of frozen blood and tissue biospecimens in pathology, biorepository, and biobank settings. Clinical biochemistry 47:258–266.

Smart C.W., Giles Jr R.H., Guynn Jr D.C. 1973. Weight tape for white-tailed deer in Virginia. The Journal of Wildlife Management 37:553–555.

Sorin A.B. 2004. Paternity assignment for white-tailed deer (*Odocoileus virginianus*): Mating across age classes and multiple paternity. Journal of Mammalogy 85:356–362.

Townsend T. W., and E. D. Bailey. 1981. Effects of age, sex and weight on social rank in penned white-tailed deer. American Midland Naturalist 106:92–101.

Trivers R. L. 1972. Parental investment and sexual selection. In: Campbell B.G., editor. Sexual selection and the descent of man 1871–1971. Aldine Publishing Company, Chicago, Illinois; p. 136–207.

Turner M.M., Deperno C.S., Booth W., Vargo E.L., Conner M.C., Lancia R.A. 2016. The mating system of white-tailed deer under Quality Deer Management. The Journal of Wildlife Management 80:935–940.

Vanpé C., Gaillard J.M., Morellet N., Kjellander P., Liberg O., Delorme D., Hewison A.J.M. 2009*b*. Age-specific variation in male breeding success of a territorial ungulate species, the European roe deer. Journal of Mammalogy. 90:661–665.

Vanpé C., Kjellander, P., Gaillard, J.M., Cosson, J.F., Galan, M. and Hewison, A.J.M., 2009*a*. Multiple paternity occurs with low frequency in the territorial roe deer, *Capreolus capreolus*. Biological Journal of the Linnean Society 97:128–139.

Weir B. S., and C. C. Cockerham. 1984. Estimating f-statistics for the analysis of population-structure. Evolution 38:1358–1370.

Weladji R.B., Gaillard J.M., Yoccoz N.G., Holand Ø., Mysterud A., Loison A., Nieminen M., Stenseth N.C. 2006. Good reindeer mothers live longer and become better in raising offspring. Proceedings of the Royal Society B: Biological Sciences 273:1239–1244.

White R.G., Rowell J.E., Hauer W.E. 1997. The role of nutrition, body condition and lactation on calving success in muskoxen. Journal of Zoology 243:13–20.

Willisch C.S., Biebach I., Koller U., Bucher T., Marreros N., Ryser-Degiorgis M.P., Keller L.F., Neuhaus P. 2012. Male reproductive pattern in a polygynous ungulate with a slow life-history: the role of age, social status and alternative mating tactics. Evolutionary Ecology 26:187–206.

Wolff J.O. 1988. Maternal investment and sex ratio adjustment in American bison calves. Behavioral Ecology and Sociobiology 23:127–133.

Wolff J.O. 1998. Breeding strategies, mate choice, and reproductive success in American bison. Oikos 83:529–544.

Wolff J.O., and D.W. Macdonald. 2004. Promiscuous females protect their offspring. Trends in Ecology & Evolution 19:127–134.

Zahavi A. 1975. Mate selection—a selection for a handicap. Journal of theoretical Biology 53:205–214.

Zeng Z.G., Song Y.L., Zhang Q. 2011. Inter-individual variations in male and female mating bonds within a population of Eld’s deer in Hainan Island, China. Mammalia 75:143–150.

Table 2.1. Microsatellites used for parentage analysis for white-tailed deer from 2008 to 2019 at the Auburn Captive Facility, Camp Hill, Alabama.

Locus	Samples	Allelic Richness	Gene Diversity[b]	F_{IS}	P[c]
Cervid1	468	14	0.87	0	1
L	467	10	0.78	0.06	0.66
BM6506	468	12	0.87	-0.01	1
N	468	16	0.87	0.19	1
INRA011	443	8	0.31	-0.06	1
BM6438	468	10	0.78	0.01	1
O	468	9	0.66	0	0.99
BL25	467	5	0.48	0	0.94
K	467	4	0.14	0.04	1
Q	466	15	0.82	0.1	1
D	465	10	0.72	0.18	0.6
OAR	468	12	0.79	-0.01	1
P	463	8	0.8	0.18	<0.001
S	466	17	0.89	0.01	1
RT5	352[a]	11	0.76	-0.04	1
RT7	352[a]	13	0.85	0.02	1
RT13	346[a]	12	0.81	0.32	<0.001
BL42	332[a]	9	0.78	-0.06	0.92

[a] Smaller sample size due to locus not being examined at ACF until 2014.

[b] Based off the Polymorphic Information Content Value.

[c] P value for Chi-Square test for deficit of homozygosity.

Table 2.2. Statistical results from T-tests and Z-Tests examining difference in skeletal body size in relation to age for female and male white-tailed deer at the Auburn Captive Facility from 2008 to 2019.

Age Comparison	1st group Mean[a]	N	2nd group Mean[a]	N	Test	Value	P Value
Females							
0.5-1.5	205.0	46	234.2	59	Z-Test	-14.90	<0.001
1.5-2.5	234.2	59	243.4	50	Z-Test	-5.03	<0.001
2.5-3.5	243.4	50	249.9	20	Z-Test	-3.39	<0.001
3.5-4.5	249.9	20	252.6	18	T-Test	-0.95	0.349
4.5-5.5	252.6	18	254.1	9	T-Test	-0.31	0.761
5.5-6.5	254.1	9	246.3	7	Z-Test	1.52	0.151
Males							
0.5-1.5	210.2	48	247.1	89	Z-Test	-16.90	<0.001
1.5-2.5	247.1	89	267.5	72	Z-Test	-10.35	<0.001
2.5-3.5	267.5	72	282.0	59	Z-Test	-6.84	<0.001
3.5-4.5	282.0	59	286.9	53	Z-Test	-2.26	0.024
4.5-5.5	286.9	53	292.6	33	Z-Test	-2.18	0.029
5.5-6.5	292.6	33	293.0	32	Z-Test	-0.13	0.891
6.5-7.5	293.0	32	292.3	18	Z-Test	0.23	0.824
7.5-8.5	292.3	18	293.1	13	T-Test	-0.2	0.846
8.5-9.5	293.1	13	293.3	7	T-Test	-0.038	0.970

[a] Measurements in centimeters.

Table 2.3. Population demographics of white-tailed deer at the Auburn Captive Facility from 2008 to 2019 based off age classes of each sex.

Age	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017	2018	2019
Total Population	71[a](35[b])	87(52)	101(63)	127(90)	127(95)	127(99)	133(107)	128(98)	133(102)	139(115)	116(99)	86(74)
Males	25(15)	40(29)	48(34)	63(50)	68(55)	67(56)	71(60)	70(56)	79(64)	75(64)	60(52)	44(39)
0.5	11(9)	16(15)	14(11)	22(21)	16(15)	15(14)	18(18)	20(17)	14(12)	15(15)	6(6)	4(4)
1.5	8(6)	10(8)	13(12)	11(8)	13(12)	12(11)	10(9)	11(11)	18(15)	11(9)	9(9)	2(2)
2.5	3(0)	8(6)	9(7)	12(11)	11(8)	10(9)	9(8)	4(3)	10(10)	14(11)	8(6)	9(9)
3.5	3(0)	3(0)	6(4)	8(6)	11(10)	9(6)	8(7)	5(4)	4(3)	8(8)	13(10)	7(5)
4.5	0	3(0)	3(0)	6(4)	8(6)	8(8)	9(6)	8(7)	5(4)	3(2)	5(5)	12(10)
5.5	0	0	3(0)	2(0)	6(4)	7(5)	6(6)	9(6)	7(7)	4(3)	3(2)	3(3)
6.5	0	0	0	2(0)	2(0)	4(3)	6(4)	5(5)	9(6)	5(5)	2(2)	2(1)
7.5	0	0	0	0	1(0)	1(0)	3(2)	5(3)	4(4)	6(5)	4(4)	2(2)
8.5	0	0	0	0	0	1(0)	1(0)	1(0)	5(3)	4(4)	3(3)	2(2)
9.5	0	0	0	0	0	0	1(0)	1(0)	1(0)	3(2)	3(3)	0
10.5	0	0	0	0	0	0	0	1(0)	1(0)	1(0)	2(2)	1(1)
11.5	0	0	0	0	0	0	0	0	1(0)	1(0)	1(0)	0
12.5	0	0	0	0	0	0	0	0	0	0	1(0)	0
13.5	0	0	0	0	0	0	0	0	0	0	0	0
Females	46(20)	47(23)	53(29)	64(40)	59(40)	60(43)	62(47)	58(42)	54(38)	64(51)	56(47)	42(35)
0.5	16(11)	8(7)	14(10)	13(12)	15(14)	11(11)	14(13)	4(2)	5(3)	16(16)	5(5)	3(3)
1.5	8(6)	14(9)	5(4)	14(10)	11(10)	14(13)	8(8)	11(9)	3(1)	4(2)	13(13)	2(2)
2.5	8(3)	6(4)	13(8)	5(4)	8(4)	8(7)	12(11)	6(6)	10(9)	3(1)	2(0)	3(3)
3.5	8(0)	7(3)	6(4)	12(7)	3(3)	6(2)	5(5)	12(11)	6(6)	9(9)	2(1)	1(0)
4.5	4(0)	6(0)	6(3)	6(4)	9(4)	2(2)	5(2)	4(4)	7(7)	6(6)	8(8)	1(1)
5.5	1(0)	4(0)	5(0)	6(3)	5(3)	8(4)	2(2)	5(2)	3(3)	6(6)	4(4)	7(7)
6.5	0	1(0)	2(0)	4(0)	5(2)	5(3)	6(2)	2(2)	5(2)	3(3)	6(6)	4(4)
7.5	1(0)	0	1(0)	2(0)	2(0)	3(1)	5(3)	5(2)	2(2)	5(2)	3(3)	6(6)
8.5	0	1(0)	0	1(0)	1(0)	2(0)	3(1)	4(3)	4(1)	2(2)	5(2)	3(3)
9.5	0	0	1(0)	0	0	1(0)	1(0)	3(1)	4(3)	4(1)	2(2)	5(2)
10.5	0	0	0	1(0)	0	0	1(0)	1(0)	3(1)	3(2)	2(1)	2(2)
11.5	0	0	0	0	0	0	0	1(0)	1(0)	2(1)	3(2)	2(1)
12.5	0	0	0	0	0	0	0	0	1(0)	1(0)	1(0)	2(1)
13.5	0	0	0	0	0	0	0	0	0	0	0	1(0)
Sex Ratio(M:F)[c]	1:2.14	1:1.63	1:1.15	1:1.24	1:0.85	1:0.94	1:0.91	1:1.1	1: 0.75	1:0.80	1:0.94	1:0.98
Density (Deer/km^2)	41	50	58	73	73	73	76	74	76	80	67	49

[a] Estimates based off candidate parents list from camera surveys, visual observation, and collection of deceased individuals.

[b] Number of individuals initially captured at 2.5 years of age or younger.

[c] Sex ratio was calculated only with individuals ≥1.5 years of age.

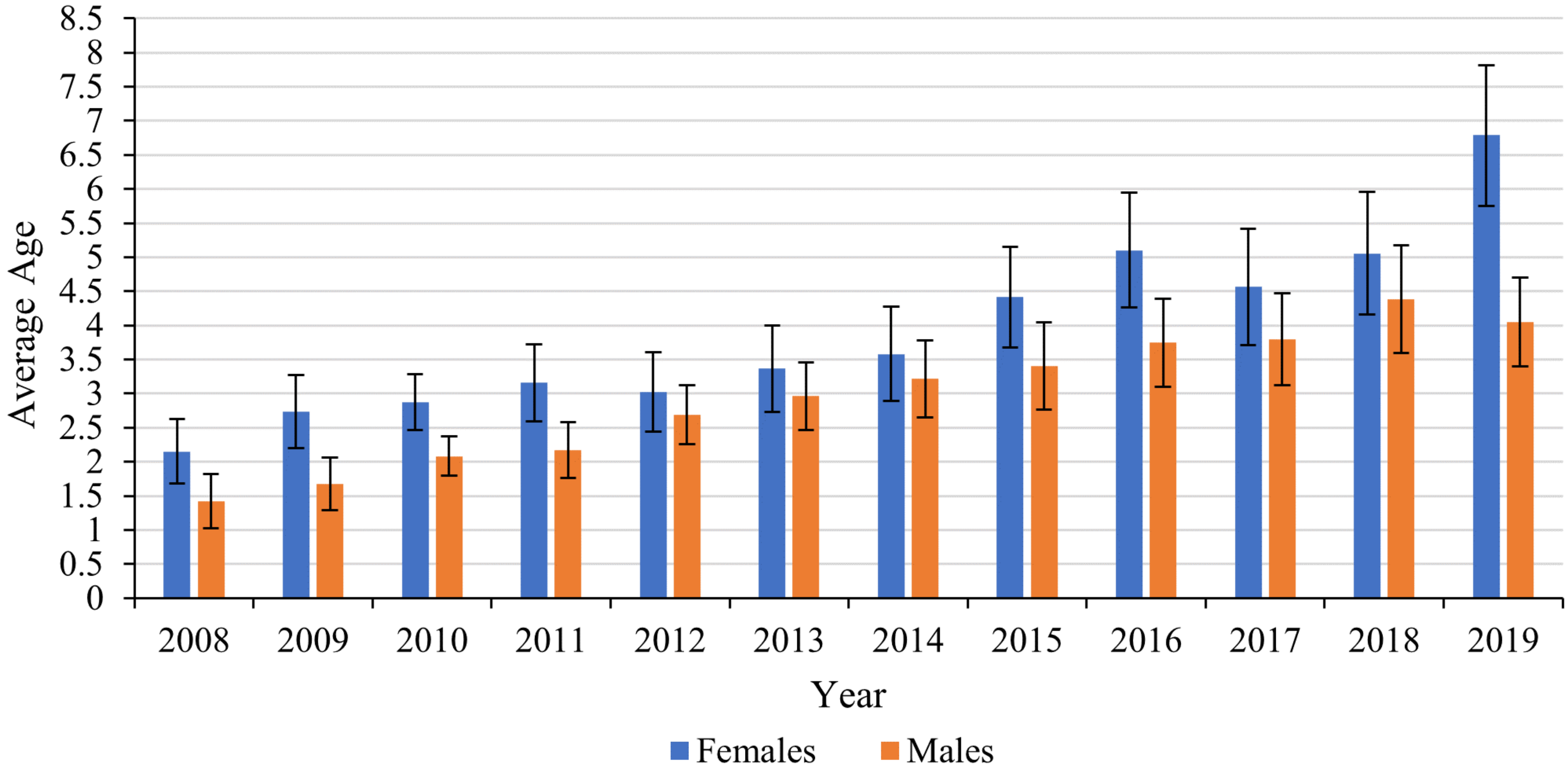

Figure 2.1. Average annual female (blue bar) and male age (orange bar) of white-tailed deer from 2008 to 2019 at the Auburn Captive Facility (ACF). Data were based off candidate mother and father lists (including fawns).

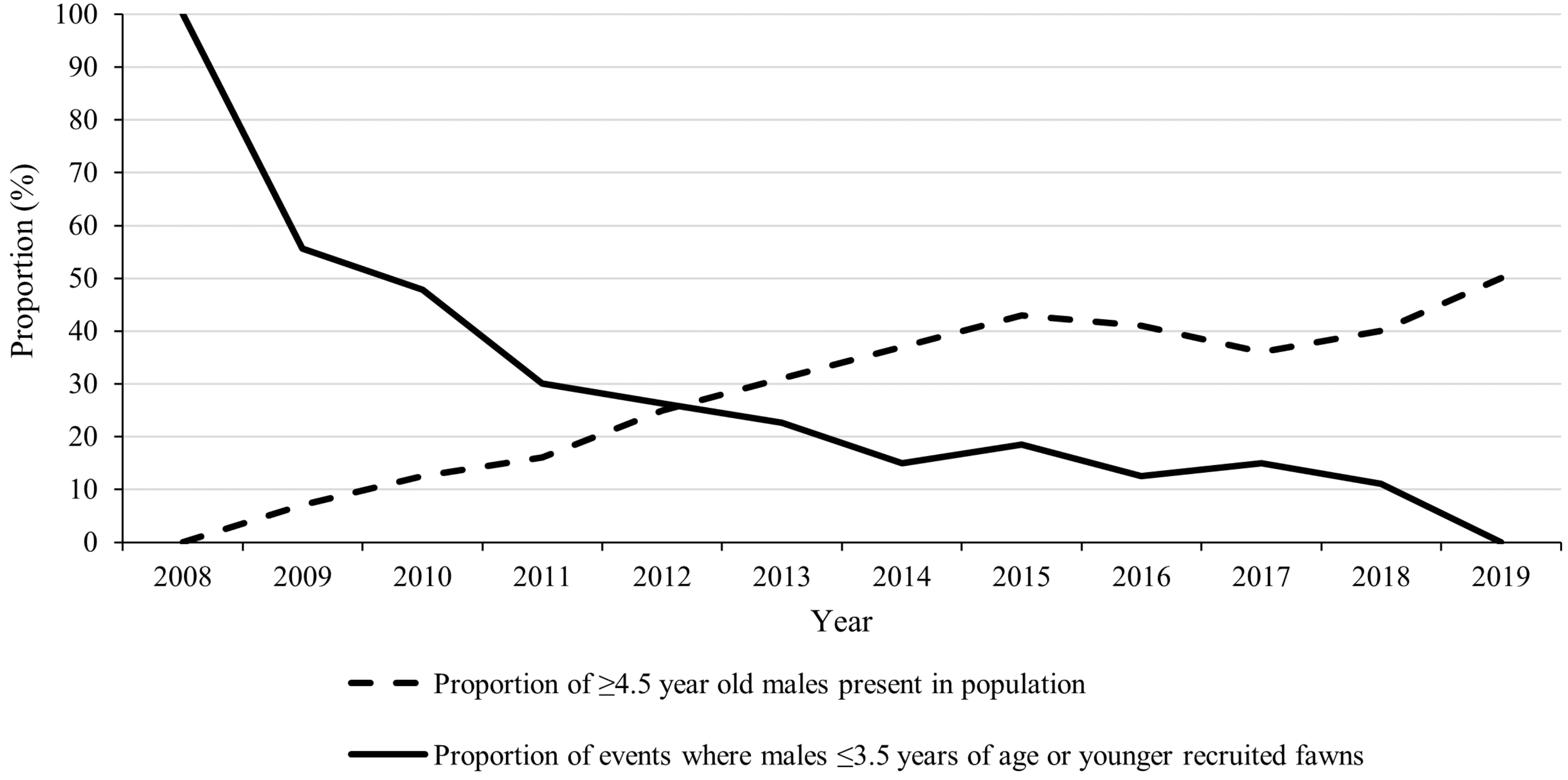

Figure 2.2. Proportion of male white-tailed deer 3.5 years of age or younger that sired a recruited fawn (solid line) and the proportion of males 4.5 years of age or older present in the population (dashed line) at the Auburn Captive Facility from 2008 to 2019.

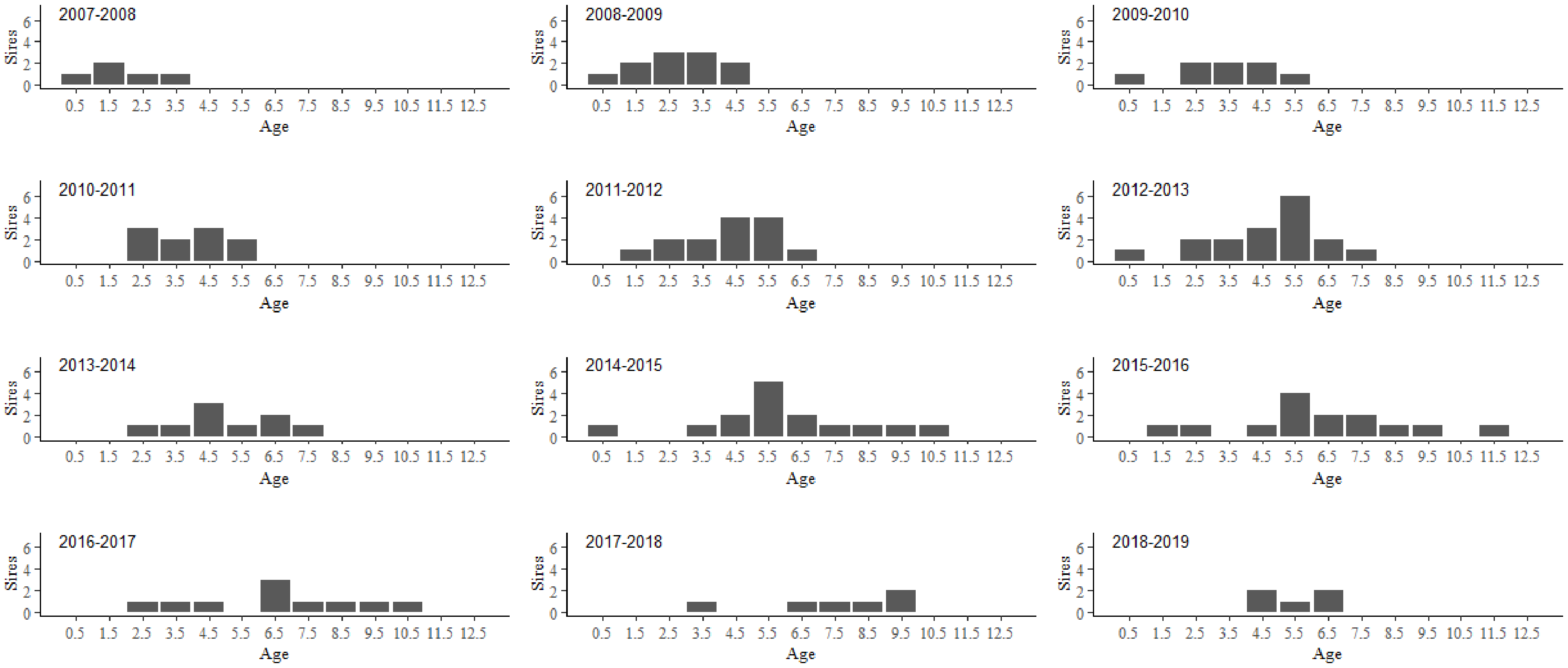

Figure 2.3. Number of male white-tailed deer in each age group that sired recruited fawns during each breeding season at the Auburn Captive Facility from 2008 to 2019.

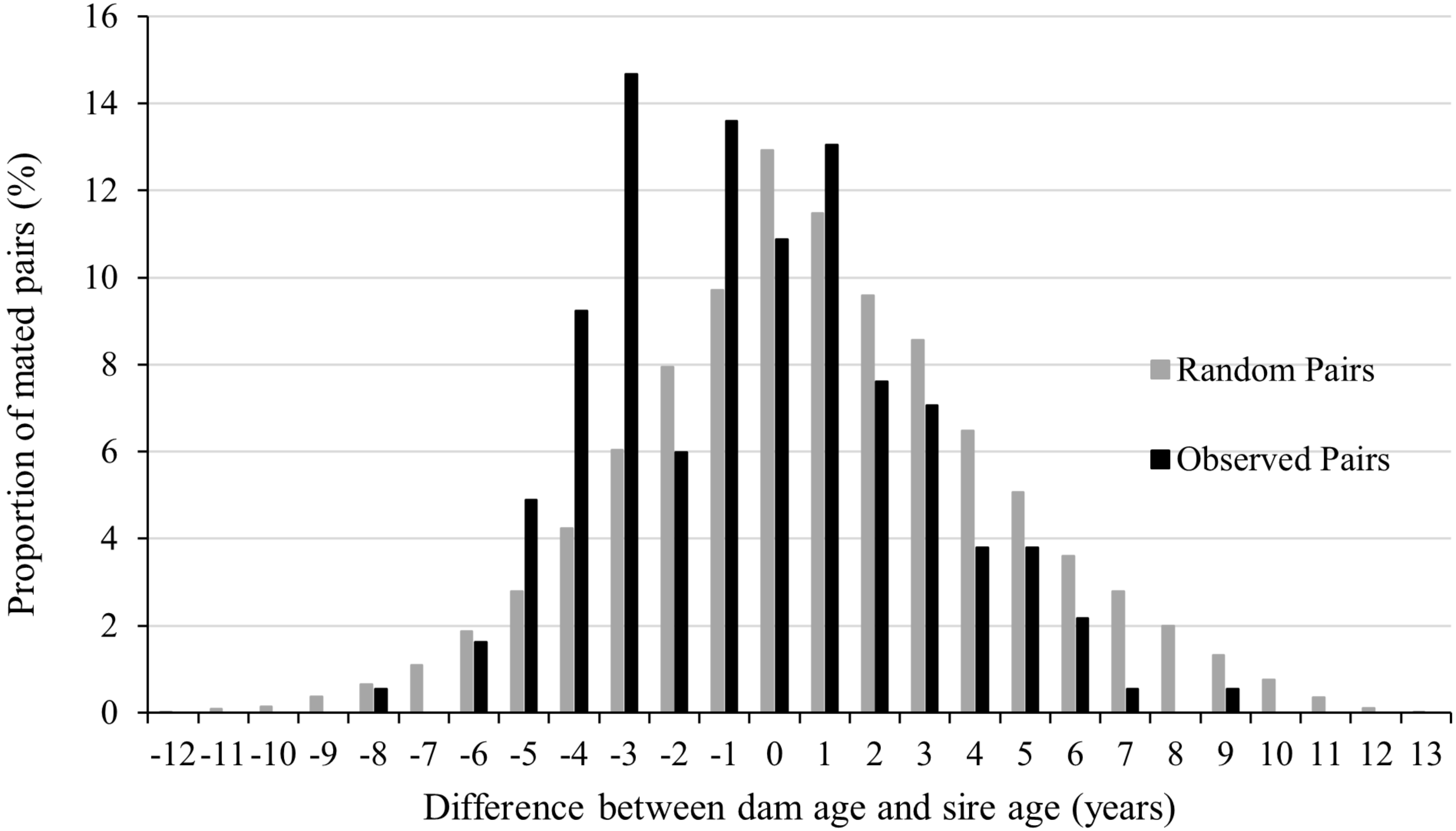

Figure 2.4. Observed age differences (black bars) of mated pairs of white-tailed deer compared to expected age differences assuming random mating (gray bars) at the Auburn Captive Facility from 2008 to 2019. Negative values represent when the male was older than the female and positive values represent when the female was older than the male.

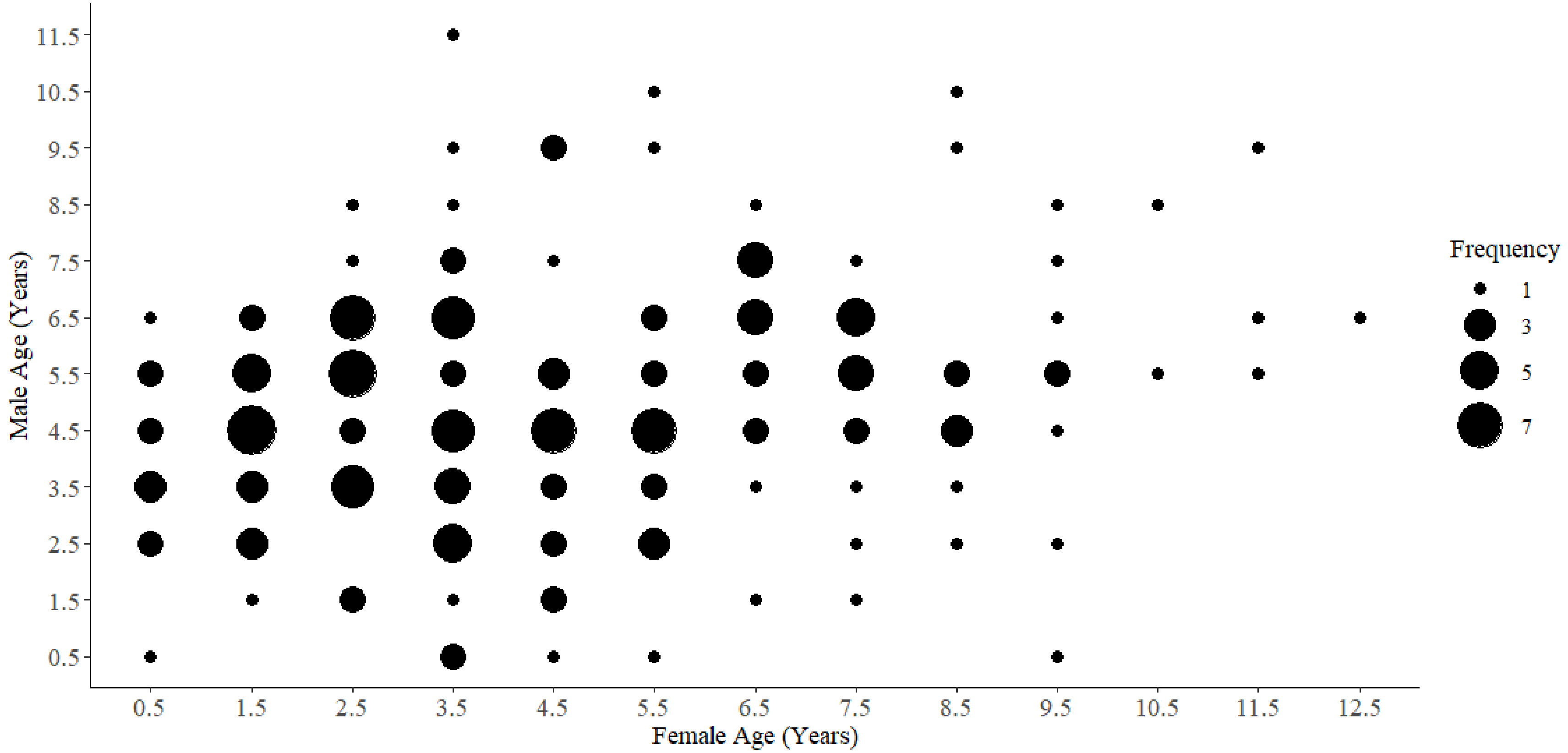

Figure 2.5. Frequency based scatter plot of age relationships of mated pairs of white-tailed deer at the Auburn Captive Facility from 2008 to 2019.

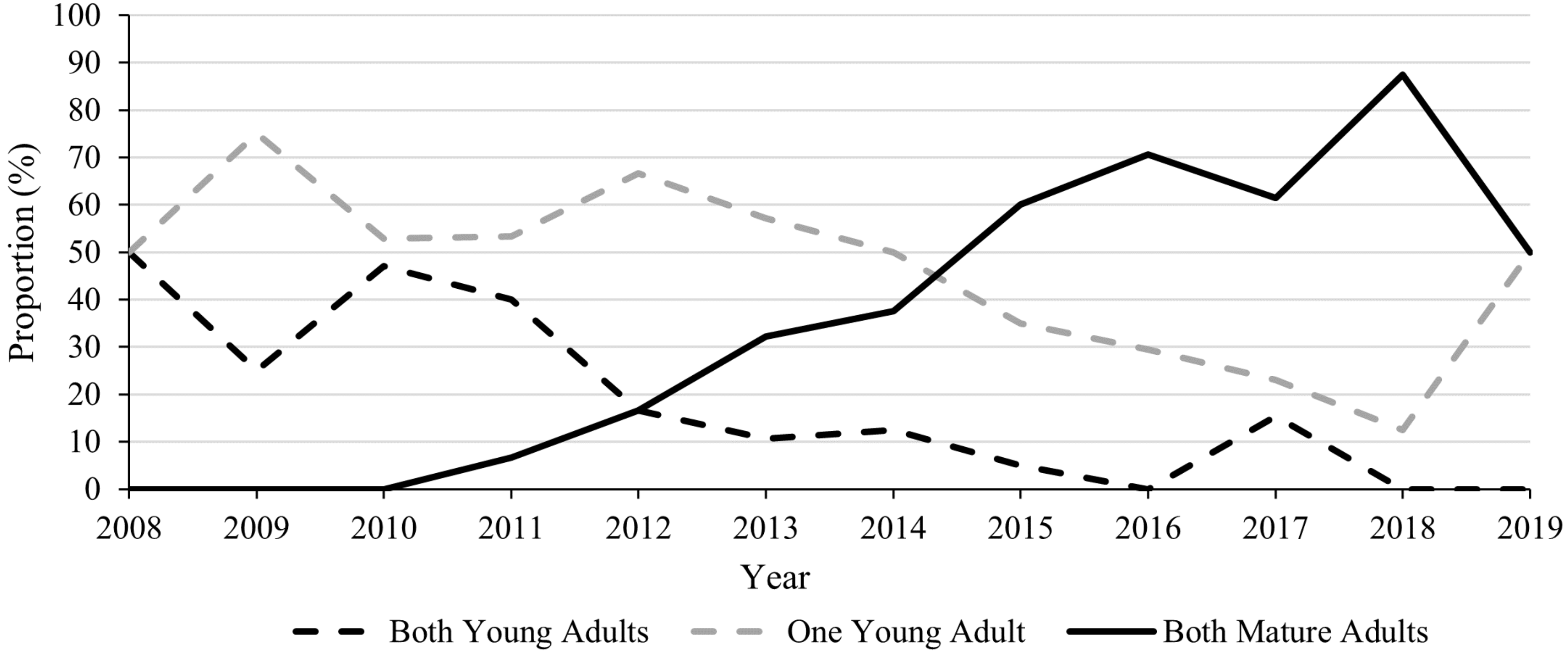

Figure 2.6. Annual proportion of mated pairs of white-tailed deer at the Auburn Captive Facility from 2008 to 2019 where both individuals were young adults (dashed black line), one individual was a young adult (dashed gray line), or both individuals were mature adults (solid black line). Males ≥5.5 and females ≥3.5 years of age were considered mature adults.

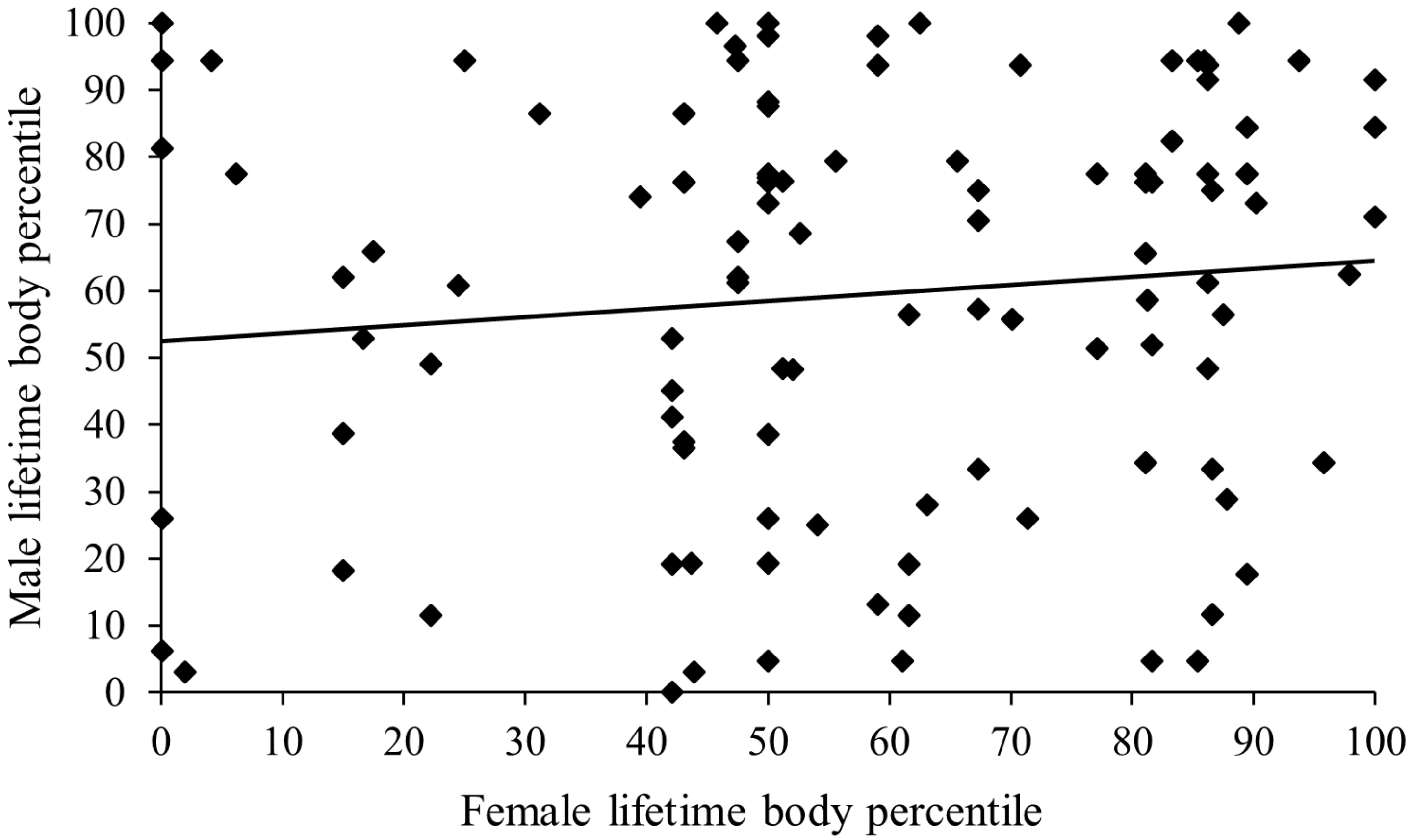

Figure 2.7. The relationship between lifetime body percentile of mated pairs of white-tailed deer at the Auburn Captive Facility from 2008 to 2019.

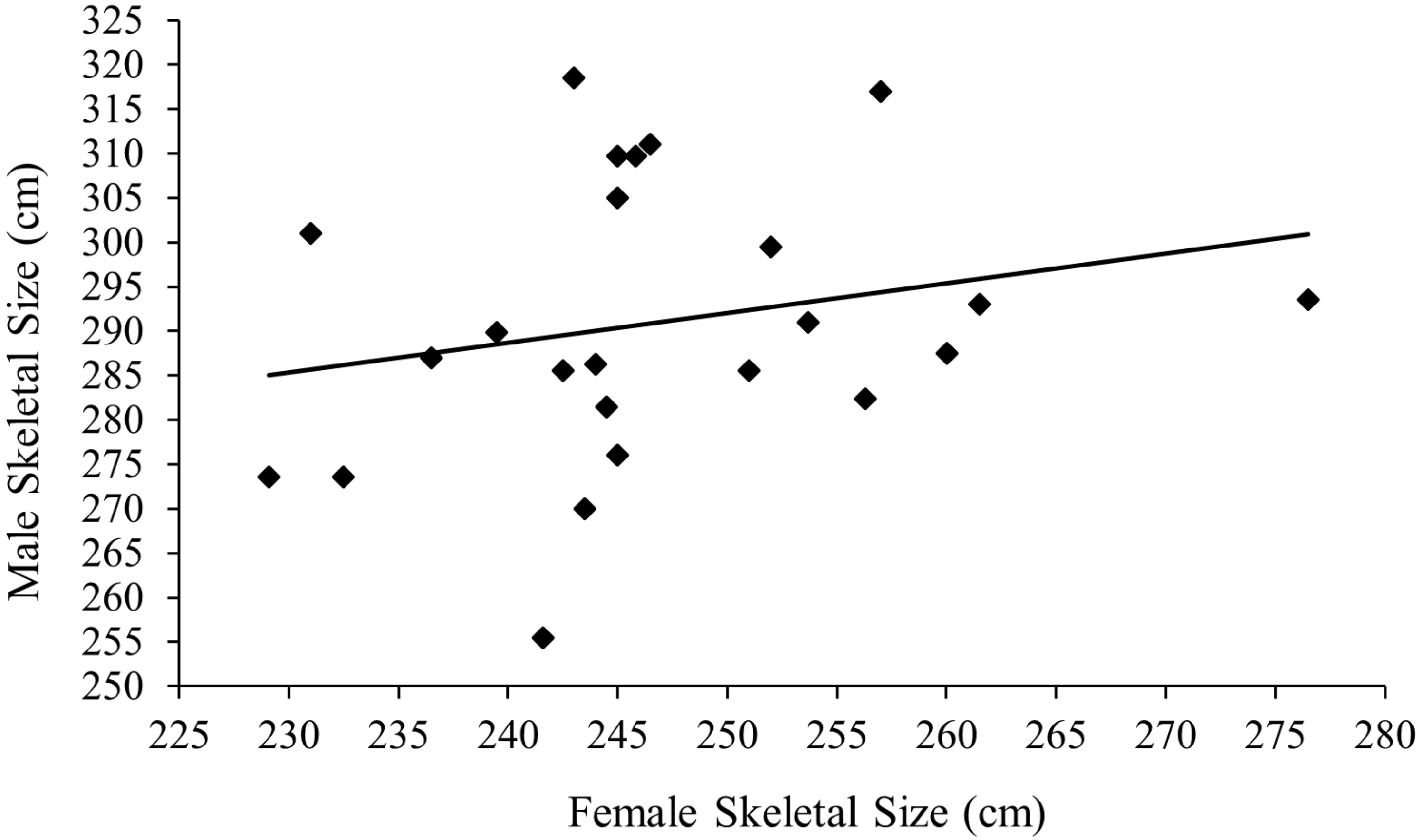

Figure 2.8. The relationship between skeletal body size of mated pairs of white-tailed deer at the Auburn Captive Facility from 2008 to 2019. Only including when measurement was collected year of.

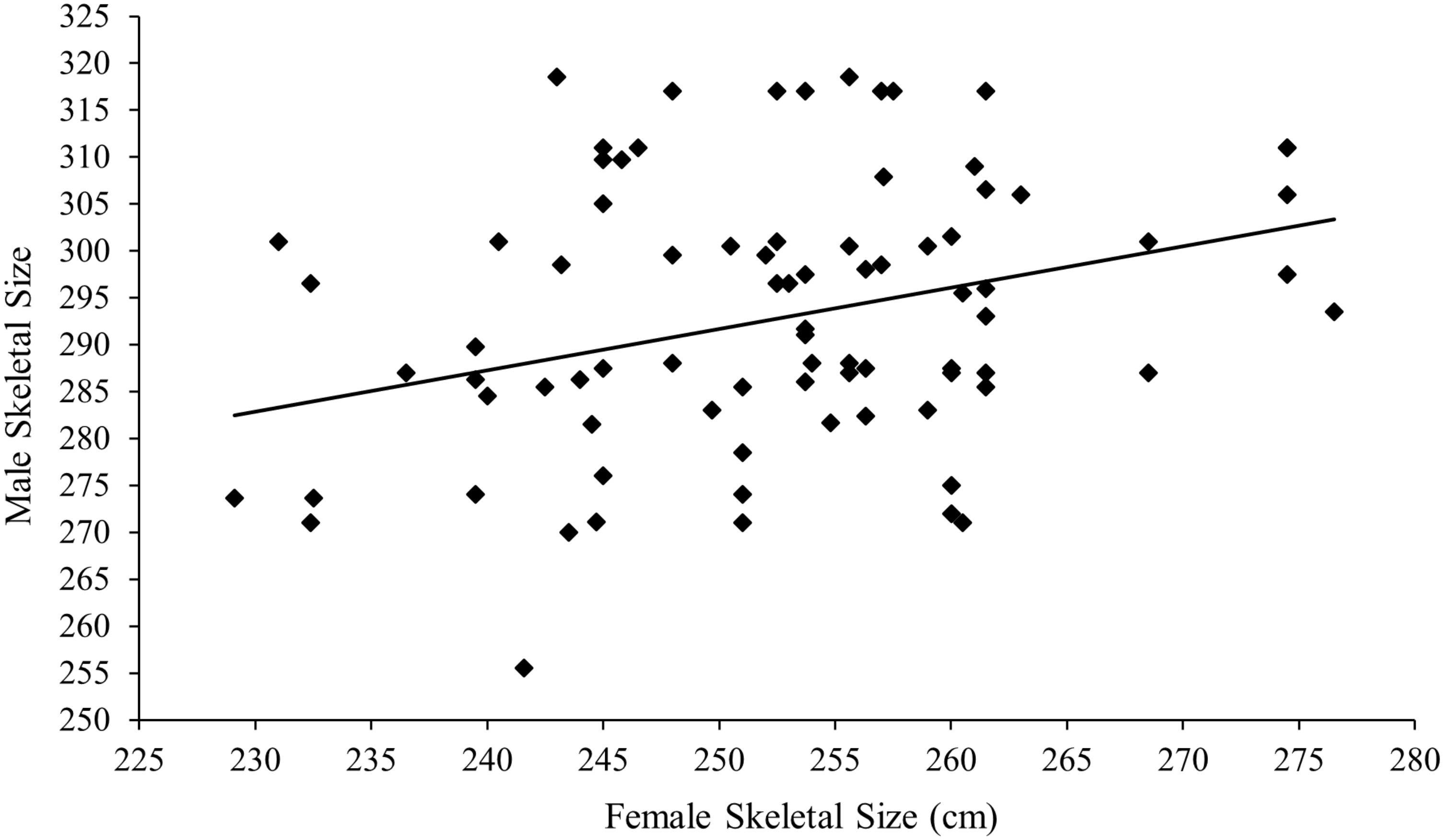

Figure 2.9. The relationship between skeletal body size of mated pairs of white-tailed deer at the Auburn Captive Facility from 2008 to 2019. Including when measurement was collected year of the breeding event or when an individual was mature and had an adult mature body measurement collected during its lifetime.

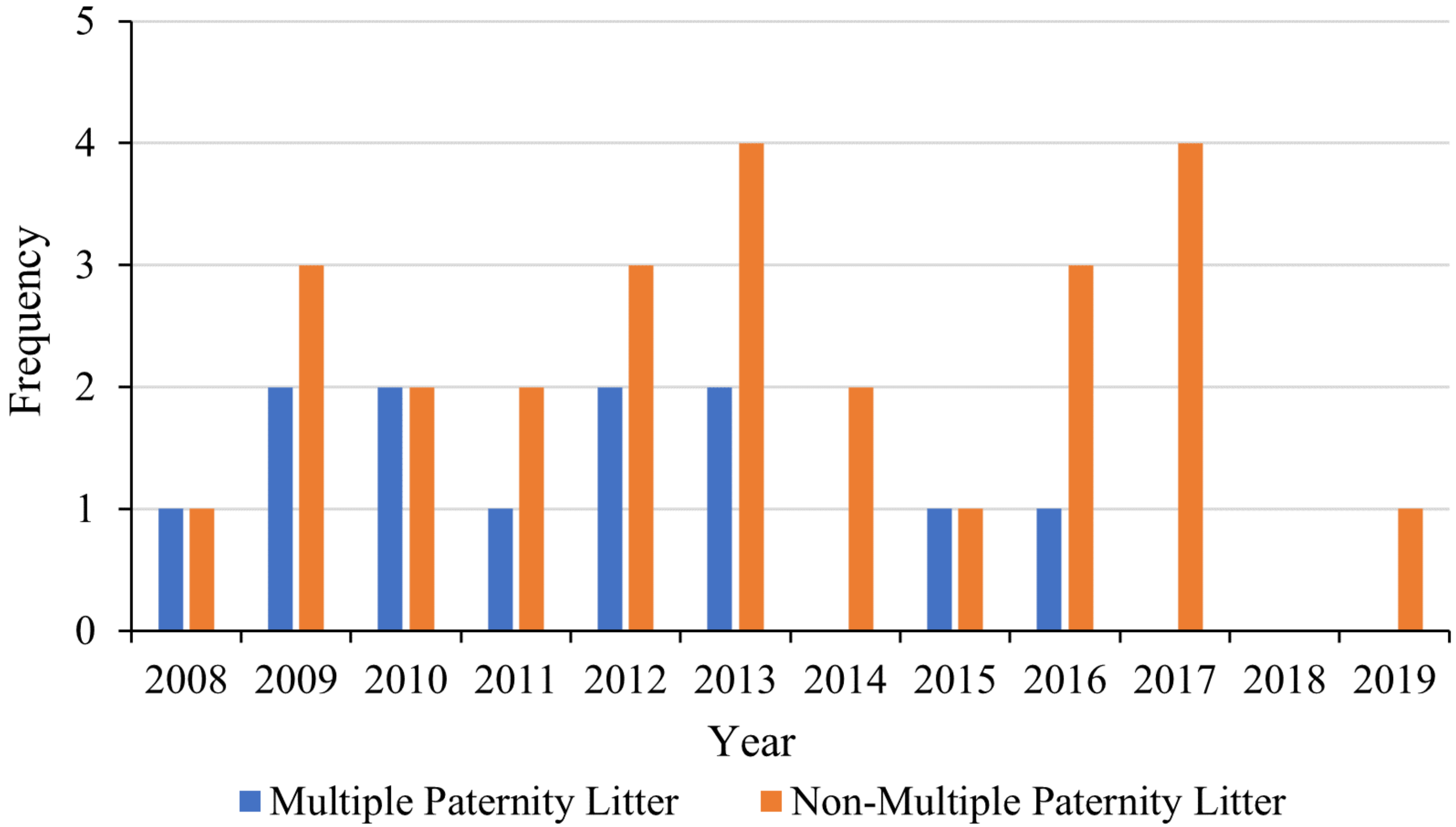

Figure 2.10. Bar chart displaying frequency of 38 litters with >1 recruited fawn at the Auburn Captive Facility from 2008 to 2019. The data are divided into two litter types: multiple paternity events (black bars) and non-multiple paternity events (gray bars).