



# Influence of maternal characteristics and reproductive history on recruitment in an iteroparous ungulate

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## Abstract

In reproductive dynamics, recruitment is a critical biological process to ensure populations remain viable. While extrinsic factors such as predation and environmental factors (e.g., droughts) have been found to strongly influence recruitment, knowledge gaps still exist 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 a mother's age, lifetime body size percentile (LBP), and past reproductive history. We found that recruitment success increased up to 6.5 years of age before declining in older age classes. We also found that age and LBP had a significant interaction such that large-bodied females had high recruitment success at younger ages that peaked around 4.5 years of age, while small-bodied females had low recruitment success at young ages and high recruitment success at older ages. We also found females that recruited a fawn in the previous year recruited 1.46 times as many fawns than females that did not recruit a fawn the year prior. 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 age of peak recruitment varies based 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

## Introduction

Recruitment is a highly important biological process in population dynamics of vertebrates. While the exact meaning of 'recruitment' depends on the context of the study, a broad definition would be the 'addition of new individuals to a population' (Gaillard

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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. 1998, 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).

In ungulates, there still exists literature gaps regarding factors that influence reproductive recruitment. For example, while numerous studies in ungulates have demonstrated the impact of 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 Conner 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) on recruitment, intrinsic factors such as maternal body weight or age have typically only examined as to how they affect fecundity (Schwartz and Hundertmark 1993; Birgersson and Ekvall 1997; Weladji et al. 2002; 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 the 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). The few studies that have been conducted on the effects of internal factors on fawn recruitment have 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 influence on recruitment; however, the literature generally lacks studies on the influence of previous reproduction on recruitment in ungulates. The fact that lactation is a costly component of reproduction is well known in white-tailed deer and other mammals (Ofstedal 1985; Robbins 1993; Hewitt 2011), and successful rearing of a fawn can negatively impact condition of a mother going into the next breeding season (Therrien et al. 2007; Ayotte et al. 2019). However, the effects of prior recruitment on the ability to recruit fawns during subsequent seasons have yet to be examined in white-tailed deer, although several studies in other ungulate species have suggested that successful recruitment the past year negatively impacts subsequent reproductive events (Clutton-Brock and Coulson 2002; Moyes et al. 2006; Martin and Festa-Bianchet 2010; Rughetti et al. 2015). Furthermore, research is very limited on the effects of recruitment success over multiple successive years and how recruiting multiple offspring in one litter may impact subsequent recruitment.

In this study, we examined reproductive patterns of adult, female white-tailed deer in a captive herd that exhibited natural breeding behavior. Because the herd was captive, 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. We hypothesized that 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 in area and was surrounded by a 2.6 m fence. The population within ACF ranged annually from 71 to 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 dactylon*), 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 to 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 to 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 125 mg/ml and given at a rate of 2.2 mg/kg) and Xylazine® (at a concentration of 100 mg/ml given at a rate of 2.2 mg/kg; 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 because the research objectives of the study focused 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  $\leq 1.5$  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 10×10 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<sup>2</sup> 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  $-80^{\circ}\text{C}$  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 (supplemental material Table S1); 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 to 2019 to account for all possible parents within ACF during a given breeding season. All females captured and ear-tagged that were 6 months of age were considered candidate mothers and remained as a candidate mother based off detection of their ear tag ID through extensive camera surveys, recapture, or confirmation through 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). We removed an individual from a candidate parent list and deemed them deceased if for the prior two years they were not detected through camera surveys or visual observation.

We only assigned parentage to individuals initially captured at  $\leq 1.5$  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. To be conservative, 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 et al. 2023; Ivy-Israel et al. 2020).

## Statistical analysis

We examined annual recruitment success for all candidate mothers in the population from 2008 to 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 grouped 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. If an individual had only one measurement during its lifetime, they were excluded from any analysis that included body size as a variable, due to our inability to create a lifetime percentile for that individual.

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 to 2019. Annual recruitment success, based off litter size of recruited fawns (e.g., 0,1,2,3 fawns), was the response variable in all models. Our model

that included all predictors variables of interest (hereafter called global model), included age, lifetime body percentile (LBP), and three separate binary categorical variables looking at facets of prior reproductive history. Looking specifically at our prior reproductive history variables, our first variable examined if a female recruited a fawn the prior year (yes or no) and labeled as PRS, our second variable examined if a female recruited a fawn in each of the two prior years (yes or no) labeled as PRS2, and finally our third variable examined specifically if a female recruited a litter of  $\geq 2$  fawns the prior year (yes or no) and labeled as PL. PL was included as a variable in our analysis due to the substantial resource requirements of twin or triplet litters. 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. Furthermore, age and LBP were examined to see if the inclusion of quadratic effects significantly improved the fit to the data based off prior literature finding evidence of age and reproductive success following a non-linear relationship in mammalian taxa (Gaillard et al. 2000, 2017; Festa-Bianchet and King 2007; Vanpé et al. 2009). To test for significance when including a quadratic term, we used a partial likelihood ratio test to compare models with and without a second degree polynomial term for the predictor variables (Murtaugh 2009). To examine the differences among age groups when accounting for all individuals (hereafter called age-only model), we split age into three categorical groups: young (0.5–1.5 years of age), prime-age (2.5–6.5 years of age), and old (7.5–13.5 years of age) based off prior reports that prime reproductive age in female white-tailed deer is from 3 to 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*, package *DHARMA*). We also tested for possible interaction terms among our predictors using a partial likelihood ratio test. After analyzing our global models, we graphed prediction curves (package *car*, package *ggplot2*) and their respective confidence intervals based off models only containing significant variables and excluded any non-significant variables (except in cases of interactions or quadratic effects). 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 to 2019 in our study population. Because we only determined maternity for known-aged individuals (captured at  $\leq 1.5$  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  $\geq 8.5$  years

old recruiting fawns; one female recruited a fawn at 12.5 years of age (Table 1). 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.,  $\geq 2$  litter involving more than one sire) where the paternity of both males could be determined at a confidence level of 95%. The average maternal age during a multiple paternity event was 5.58 years (SE=0.72).

In our global model, a partial likelihood ratio test determined that fit to the data was significantly improved when we included a quadratic effect for age ( $P < 0.001$ ), but not LBP ( $P = 0.193$ ). We also found a significant interaction term between our age variables (linear and quadratic) and LBP ( $P = 0.016$ ). We found 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, we found no collinearity among our main variables (VIF Age=1.09, VIF LBP=1.05, VIF PRS=1.68, VIF PRS2=1.50, VIF PL=1.36). The random effect for breeding season (Bszn) was not significant ( $P > 0.999$ ) and we excluded it from further analysis. The random effect for individual (ID) was also not significant ( $P > 0.999$ ) but was retained in analysis due to the 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. Our global model indicated 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 2). However, we did find significant linear ( $P = 0.045$ ) and quadratic ( $P < 0.001$ ) relationships between age and annual fawn recruitment. Furthermore, we found a significant interaction between the linear age variable and LBP ( $P = 0.005$ ), but not the quadratic age variable and LBP ( $P = 0.415$ ). Conducting model predictions when only including significant variables we found that individuals with a greater percentile score (larger body size) had greater recruitment success (predicted number of annual recruited offspring)

**Table 1** Age-specific recruitment of fawns with maternal-known parentage at the Auburn Captive Facility from 2008 to 2019

Age-class	Potential mothers <sup>a</sup>	Known mothers <sup>b</sup>	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

<sup>a</sup>Based off candidate mother lists for each year

<sup>b</sup>Based of Parentage 1.1d with a minimum confidence threshold of 95%



**Table 2** Generalized linear model results comparing annual recruitment success to lifetime body percentile (LBP), prior recruitment success for the past year (PRS) and past 2 years (PRS2), if the prior litter had  $\geq 2$  fawns (PL), linear and quadratic age, and an interaction term between lifetime body percentile and age (LBP:Age, LBP:Age<sup>b</sup>). All data were obtained from white-tailed deer at the Auburn Captive Facility from 2008 to 2019. Model based off sample size of 249 breeding season observations for 37 individuals

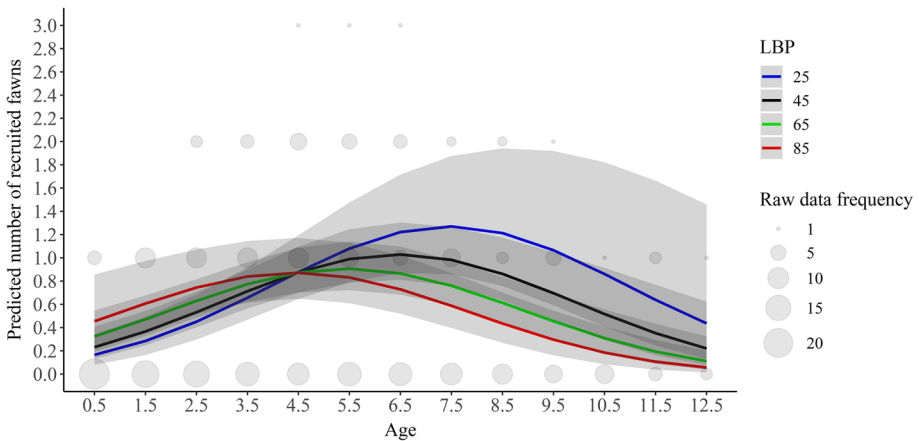
Parameter	Value <sup>a</sup>	CL <sup>a</sup>	N	SE	Z-Value	P-Value
Intercept	0.73	0.55–0.97	249	0.14	−2.15	0.032
LBP	0.90	0.71–1.13	249	0.12	−0.94	0.348
PRS	1.14	0.73–1.77	249	0.23	0.58	0.564
PRS2	0.88	0.52–1.48	249	0.27	−0.49	0.621
PL	1.08	0.63–1.84	249	0.27	0.28	0.782
Age	1.27	1.01–1.61	249	0.12	2.01	0.045
Age <sup>b</sup>	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 <sup>b</sup>	1.11	0.87–1.41	249	0.12	0.82	0.415

$R^2 = 0.246$ , Residual degrees of freedom = 239

<sup>a</sup> All betas and confidence limits (CL) were exponentiated

<sup>b</sup> Quadratic age

at younger ages (0.5–4.5 years of age) compared to individuals with lesser percentile scores (Fig. 1). However, we found that an inflection point occurred between 4.5 and 5.5 years of age, where older individuals (5.5–12.5 years of age) with lower percentile



**Fig. 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 individuals. 95% confidence intervals are shown shaded in grey for each respective prediction curve. Original data is portrayed graphically through the use of a frequency bubble chart display to account for overlapping points. Recruitment success within this study was based off 260 parentage-known fawns with predictions adjusted to account for a further 49 fawns where parentage was determined but below the 95% confidence threshold



scores had greater recruitment success than individuals with greater percentile scores (Fig. 1).

To include individuals with no body size scores, we reran our analysis with a model including all predictor variables except LBP, which resulted in 629 individual breeding season observations for 149 individuals. We found linear ( $P < 0.001$ ) and quadratic ( $P < 0.001$ ) age to be significant but found no relationship between annual fawn recruitment and PRS2 ( $P = 0.948$ ) or PL ( $P = 0.927$ , Table 3a). However, in this model PRS was found to have a near-significant positive trend ( $P = 0.063$ ). Rerunning this model excluding PRS2 and PL to further increase sample size (637 breeding season observations for 151 individuals), we found PRS had a significant positive relationship with recruitment success. Specifically, when PRS was significant within the model, if a female recruited a fawn the prior year, she recruited 1.46 (1.03–2.07; 95% C.L.) times as many fawns than females who did not recruit a fawn the prior year ( $P = 0.032$ ; Table 3b). Once again, within this model we also found a significant linear ( $P < 0.001$ ) and quadratic ( $P < 0.001$ ) relationship between age and annual fawn recruitment. Conducting model predictions when only including significant variables, we observed that as age increased, the annual predicted number of recruited fawns increased until it peaked at 5.5–6.5 years of age at 0.88 recruited fawns, then decreased (Table 3b; Fig. 2).

When running our age-only model (linear and quadratic age), we had 667 individual breeding season observations for 156 individuals. Similar to our previous findings, both

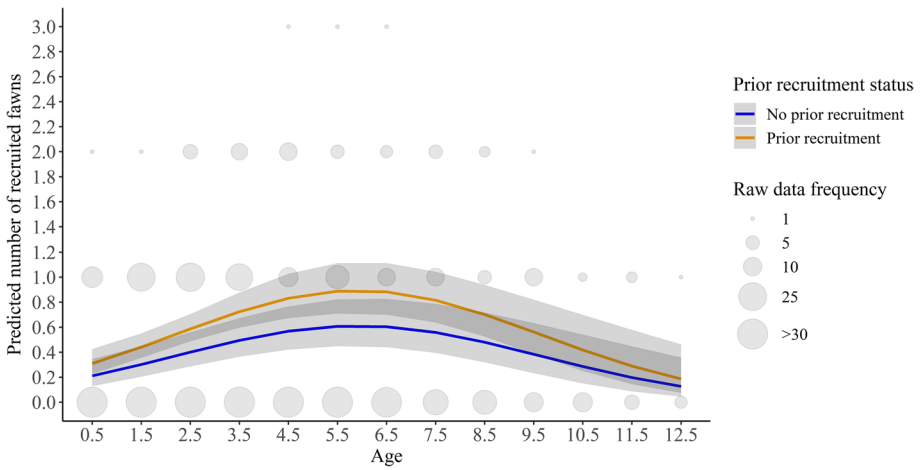
**Table 3** Generalized linear model results, excluding LBP, comparing annual recruitment success to prior recruitment success for the past year (PRS) and past two years (PRS2), if the prior litter had  $\geq 2$  fawns (PL), and linear and quadratic age (section a). Additional model included within table excluding PRS2 and PL to increase sample size (section b). All data were obtained from white-tailed deer at the Auburn Captive Facility from 2008 to 2019. Full model based off sample size of 629 breeding season observations of 149 individuals, while the reduced model, excluding PRS2 and PL, contained a sample size of 637 breeding season observations for 151 individuals

Parameter	Value <sup>a</sup>	CL <sup>a</sup>	N	SE	Z-Value	P-Value
<b>a. Full model</b>						
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 <sup>c</sup>	0.72	0.62–0.84	629	0.078	–4.24	<0.001
$R^2 = 0.147$ , Residual degrees of freedom = 622						
<b>b. Model excluding PRS2 and PL to increase sample size<sup>b</sup></b>						
Intercept	0.43	0.35–0.53	637	0.10	–8.22	<0.001
PRS	1.46	1.03–2.07	637	0.18	2.15	0.032
Age	1.55	1.28–1.88	637	0.10	4.57	<0.001
Age <sup>c</sup>	0.72	0.62–0.84	637	0.08	–4.29	<0.001
$R^2 = 0.152$ , Residual degrees of freedom = 632						

<sup>a</sup> All betas and confidence limits (CL) were exponentiated

<sup>b</sup> Model utilized for graphing predictions in Fig. 2

<sup>c</sup> Quadratic age



**Fig. 2** Predicted relationship of annual recruitment success of female white-tailed deer in relation to maternal age and prior year’s reproductive history (PRS) based off data at the Auburn Captive Facility from 2008 to 2019. Data were based off a model of 637 breeding season observations of 151 individuals. 95% confidence intervals are shown shaded in grey for each respective prediction curve. Original data is portrayed graphically through the use of a frequency bubble chart display to account for overlapping points. Recruitment success was based off 260 parentage-known fawns with predictions adjusted to account for a further 49 fawns where parentage was determined but below the 95% confidence threshold

**Table 4** Generalized linear model results comparing annual recruitment success to age. Non-categorical age model (section a) includes just linear and quadratic age. Categorical age model (sections b and c) includes three female age groups: Young (0.5–1.5), Prime (2.5–6.5), and Old (7.5–12.5). All data were obtained from white-tailed deer at the Auburn Captive Facility from 2008 to 2019. Models based off sample size of 667 (section a) and 668 (section b and c) breeding season observations respectively of 156 individuals

Parameter	Value <sup>a</sup>	CL <sup>a</sup>	N	SE	Z-Value	P-Value
<b>a. Non-categorical age</b>						
Intercept	0.47	0.39–0.56	667	0.10	−7.91	<0.001
Age	0.69	0.60–0.79	667	0.07	−5.35	<0.001
Age <sup>b</sup>	1.66	1.39–2.0	667	0.09	5.53	<0.001
<i>R<sup>2</sup> = 0.198, Residual degrees of freedom = 663</i>						
<b>b. Categorical: Young age group as reference</b>						
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
<i>R<sup>2</sup> = 0.183, Residual degrees of freedom = 664</i>						
<b>c. Categorical: Old age group as reference</b>						
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
<i>R<sup>2</sup> = 0.183, Residual degrees of freedom = 664</i>						

<sup>a</sup> All betas and confidence limits (CL) were exponentiated

<sup>b</sup> Quadratic age

linear and quadratic age terms were significant ( $P < 0.001$ ), and our predicted peak annual recruitment occurred from 5.5 to 6.5 years of age (Table 4a). Furthermore, with our age-only model when dividing age into categorical groups (i.e., Young, Prime-age, Old), and still excluding all other variables, prime-age adults recruited 2.71 (1.94–3.79; 95% C.L.) times as many fawns as young adults ( $P < 0.001$ ), and old adults recruited 2.17 (1.41–3.32; 95% C.L.) times as many fawns as young adults ( $P < 0.001$ , Table 4b). Changing the reference group to old adults, we found prime-age adults recruited 1.25 (0.90–1.75; 95% C.L.) times as many fawns as old adults; however, the differences were not statistically significant ( $P = 0.192$ ; Table 4c).

Because PRS had a significant positive effect on annual fawn recruitment, we further 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 female recruited a triplet litter at 6.5 years old, and then recruited a twin litter the subsequent year. From the age of 2.5–10.5 one female recruited nine fawns. When comparing life history traits between consecutive recruiters and other females using a Welch Two Sample *t*-test, we found consecutive recruiters lived 5.23 (3.12–7.34; 95% C.L.) years longer ( $t = 5.19$ ;  $P < 0.001$ ), recruited the first fawn of their reproductive lifespan 0.91 (0.093–1.74; 95% C.L.) years earlier ( $t = 2.26$ ;  $P = 0.030$ ), and recruited their last fawn 4.28 (2.0–6.56; 95% C.L.) years later ( $t = 3.87$ ;  $P < 0.001$ ) than females who never recruited fawns in consecutive years (Table 5). Furthermore, while not statistically significant, consecutive recruiters on average were 20.20 (– 2.41–42.80; 95% C.L.) body size percentiles larger ( $t = 1.94$ ;  $P = 0.076$ ) and had 7.78 (– 11.48–27.04; 95% C.L.) fewer parasites ( $t = 1.21$ ;  $P = 0.305$ ) than other females. When examining known males that bred with both groups using a Two Sample *z*-tests, we found that sires that bred with consecutive recruiters were on average 0.98 (0.0013–1.96; 95% C.L.) years younger than sires that bred with non-consecutive recruiters ( $z = 1.96$ ;  $P = 0.049$ ). Furthermore, sires that bred with non-consecutive recruiters were 0.63 (–10.66–11.92; 95% C.L.) body size percentiles larger than sires that bred with consecutive recruiters, but this was not statistically significant ( $z = 0.11$ ;  $P = 0.913$ ).

## Discussion

The data did not fully support our original hypothesis that age would have a positive effect on recruitment success. Instead, our findings are consistent with other studies in mammals indicating that reproductive performance in a population follows a parabolic curve: increasing until prime reproductive age, plateauing and then decreasing with advanced age and the onset of senescence (Gaillard et al. 2017). Our findings in this captive herd are similar to other studies of captive and wild populations of white-tailed deer, where reproductive performance was found to increase with age (Mundinger

**Table 5** 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 were obtained within the Auburn Captive Facility from 2008 to 2019

Parameter	Consecutive N	Consecutive $\bar{x}$	Non-consecutive N <sup>a</sup>	Non-consecutive $\bar{x}$	Test statistic	P-Value
Female characteristics						
Longevity	15	9.33	30	4.10	5.19 <sup>b</sup>	< 0.001
First recruitment	28 <sup>c</sup>	2.29	25	3.20	2.26 <sup>b</sup>	0.030
Last recruitment	15	7.73	11	3.45	3.87 <sup>b</sup>	< 0.001
Parasite load <sup>d</sup>	17	3.51	4	11.29	1.21 <sup>b</sup>	0.305
LBP <sup>e</sup>	24	57.14	9	36.94	1.94 <sup>b</sup>	0.076
Male characteristics						
Sire age	158	4.99	30	5.97	1.96 <sup>f</sup>	0.049
Sire LBP <sup>e</sup>	153	58.96	26	59.59	0.11 <sup>f</sup>	0.913

<sup>a</sup> Excluded individuals where full life history unknown and unable to determine if consecutively recruited in lifetime

<sup>b</sup> Welch two sample t-test

<sup>c</sup> Excluded consecutive recruiters where full reproductive history was unknown

<sup>d</sup> Average count of ectoparasites present on designated spots of sedated animal

<sup>e</sup> Lifetime body percentile

<sup>f</sup> Two sample z-test

1981; Dusek et al. 1989; Neuman et al. 2016). While we were unable to quantify rate of fawn predation or possible stress induced from density, similar studies have found reproductive performance improves with age due to enhanced 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 (Langenau and Lerg 1976; Ozoga and Verme 1982; Ozoga et al. 1982; Smith 1987). We observed a decline in annual recruitment success beginning at about 7 years of age in the population. Declines in reproductive performance, often described as reproductive senescence (Kirkwood and Austad 2000), have primarily been observed in ungulates from the standpoint of declines in fecundity (e.g., offspring birth mass, litter size at conception), with declines occurring from 8 to 12 years of age, depending on species: 8 years of age in reindeer (*Rangifer tarandus*; Weladji et al. 2002), soay sheep (*Ovis aries*; Robinson et al. 2006), and alpine chamois (*Rupicapra rupicapra*; Morin et al. 2016), 9 years in fallow deer (*Dama dama*; San José et al. 1999) and red deer (*Cervus elaphus*; Nussey et al. 2006), and 12 years of age in moose (*Alces alces*; Ericsson et al. 2001). In white-tailed deer, prior studies have noted declines in fecundity and neonate survival at  $\geq 8$  years of age (DelGiudice et al. 2007; Ayotte et al. 2019) and general declines in number of weaned offspring at advanced ages (Nixon and Mankin 2015), but no conclusive evidence has yet been made regarding reproductive senescence. From the standpoint of observing different reproductive components regarding senescence, findings by us and studies mentioned previously may indicate that fertility persists longer than the ability to recruit fawns in white-tailed deer. However, we must acknowledge that supplemental feed and a high population density may enhance or weaken reproductive performance in advanced age classes, and further research is

warranted before firm conclusions can be made regarding reproductive senescence from the perspective of recruitment.

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 recruitment peaked at younger ages for large individuals and at older ages for small-bodied deer. 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; Ditchkoff 2011). Prior to that, a female undergoes a tradeoff: reproduce at the cost of somatic growth or delay reproductive investment to maximize growth and future residual reproductive value (Fisher 1930; Williams 1966). Similar to 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 to mitigate the costs of reproduction (Hewison 1996; Sand 1996; Monteith et al. 2014; Flajšman et al. 2017; Festa-Bianchet et al. 2019). Furthermore, in captive white-tailed deer that were supplementally fed, 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. High reproductive success at a young age may negatively impact reproduction and survival later in life, potentially due to reduced body condition (Williams 1966; Stearns 1992) and accumulation of physiological damage and deterioration (Kirkwood 1977; Kirkwood and Rose 1991; McNamara et al. 2009). Reproducing at an early age and physically deteriorating at a quickened rate is often regarded as a live fast, die young reproductive strategy (Bonduriansky et al. 2008). Most evidence for this strategy, based off decreased survival and an increased rate of reproductive senescence, in female vertebrates has been observed in birds (Gustafsson and Pärt 1990; Reid et al. 2003; Charmantier et al. 2006; Reed et al. 2008) and rodents (Descamps et al. 2006; Rubach et al. 2020). In iteroparous mammalian species, the live fast die young strategy has been more commonly described for males (Robinson et al. 2006; Lemaître et al. 2018; Gomes et al. 2021), with only limited evidence in females (Reiter and Le Boeuf 1991; Nussey et al. 2006; Hayward et al. 2014). However, further research is warranted to support evidence for this strategy due to the fact we did not measure body mass in our study and were unable to determine if there was a decline in physical condition past 4.5 years of age that may have contributed to a decrease in recruitment success.

Small-bodied individuals may have low recruitment success at younger ages due to an inability to cope with the competing demands of lactation and somatic growth even with supplemental feed available. It has previously been reported in non-captive populations that white-tailed deer (Therrien et al. 2007; Ayotte et al. 2019) and other ungulate species (Sæther and Haagenrud 1983; Green and Rothstein 1991; Kirkpatrick et al. 1993; Cameron 1994; White et al. 1997) will adopt conservative reproductive strategies that value self over offspring when nutritionally stressed. For example, young, and small-bodied female ungulates generally produce low yields of milk (Arman et al. 1974; Blaxter and Hamilton 1980; Strickland et al. 2008), often resulting in greater offspring mortality (Verme 1962; Langenau and Lerg 1976; Guinness et al. 1978; Mech and McRoberts 1990). While females within ACF are unlikely nutritionally stressed due to access to supplemental feed, smaller bodied individuals may still divert a greater proportion of resources towards growth at younger ages. It is well documented that small-bodied females in multiple mammalian taxa will prolong growth at the expense of reproduction early in life (Descamps et al. 2006; Marcil-Ferland et al. 2013). However, our data seems to suggest that once an individual

has reached maximized skeletal growth, they are then able to invest sufficient or a greater proportion of resources towards reproduction.

We observed that prior recruitment success (PRS) had a positive effect on subsequent recruitment, contrary to our original hypothesis. PRS was not significant in our global model, but this was likely due to 40% of our consecutive recruiters being excluded in this analysis because of no LBP score. While we were unable to detect significance of PRS2 within any of our models, likely due to low sample size, it was surprising we did not detect a significant negative effect of PL on recruitment success; instead finding a non-significant positive effect. Prior research of mammalian taxa indicates the nutritional demands and resource expenditure of rearing offspring is extremely high (Andersson et al. 1980; Clutton-Brock et al. 1989), which should leave a female in suboptimal condition when entering the subsequent breeding season (Stearns 1992). Indeed, Therrien et al. (2007) studying captive white-tailed deer found that if a female weaned a fawn the prior year, they gained less mass per day compared to females that did not. This led them to speculate that costs of prior reproduction on maternal mass could negatively impact subsequent reproduction (Therrien et al. 2007), possibly through a reduction in fawn birth mass as documented in other studies (Monteith et al. 2009; Michel et al. 2015). Similarly, reproductive declines have been observed after successfully rearing offspring the prior year in alpine ibex (*Capra ibex*; Rughetti et al. 2015), elk (*Cervus canadensis*; 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. 2009a), mountain goat (*Oreamnos americanus*; Hamel et al. 2009a), 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. 2009a), and soay sheep (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. (2009a) 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 suggests 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 through examination of random effects, we observed significant differences in life history traits and mate characteristics between consecutive recruiters and non-consecutive recruiters; specifically, longevity, age of primiparity in recruitment, and the average age of the sire. Our observation that consecutive recruiters on average mated with younger males is a fascinating finding that warrants further research due to mate selection and assortative mating being documented at ACF prior (Swartout 2022). Regarding difference in life history traits, it is well established in ungulates and other iteroparous mammals that high reproductive performance is highly correlated with longevity, where long-lived individuals also have the greatest lifetime reproductive success (Bérubé et al. 1999; Kruuk et al. 1999; Weladji et al. 2006; Le Boeuf et al. 2019; Mclean et al. 2019). However, the debate on what causes variation in individual longevity and 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. 2009a, 2009b; 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, at least partially, 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; Toïgo et al. 2002; Weladji et al. 2008; Hamel et al. 2009a). 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, <50% of mothers consecutively recruited fawns during their lifetime. This result suggests to us that heterogeneity in quality among individuals exists, and a subset of high-quality individuals in the population annually recruit a large majority of the fawns.

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**Availability of data and material** Data can be made available upon request to the authors.

## Declarations

**Conflicts of interest** The authors declare no conflicts of interest.

**Ethics approval** 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).



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