

The Influence of Population Demographics on White-tailed Deer Fawning Season

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Abstract: White-tailed deer (*Odocoileus virginianus*) are one of the most abundant and well-studied ungulates in North America. Few studies, however, have examined how population demography affects the fawning season, which may be influenced by age structure and adult sex ratio of the population. From 2010 to 2013, we used vaginal implant transmitters (VITs) to record the birth date of fawns born within a 174-ha captive facility to elucidate how population demography affects fawning season. We documented an earlier shift in fawning season as male age structure increased from a mean of 2.74 years old in 2010 to 3.92 years old in 2013. Prior to the shift, the mean fawning date was 12 August, and after an increase in population age structure, the mean fawning date was 30 July. An earlier fawning season may be important for neonatal survival, especially in areas of the Southeast where coyotes (*Canis latrans*) may limit recruitment. The effect of male age structure on the timing and duration of the fawning season has yet to be firmly established, but we predict managers can increase neonate development and survival by increasing male age structure.

Key words: white-tailed deer, fawning, vaginal implant transmitter, age structure

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Management of white-tailed deer (*Odocoileus virginianus*) has increased over the last two decades and has shifted from traditional management for maximum sustained yield to herds managed for quality (Miller and Marchinton 1995). Quality deer management (QDM) was designed to increase overall herd condition by harvesting an appropriate amount of antlerless deer relative to available habitat and protecting young males from harvest (Miller and Marchinton 1995). Increases in antler size and hunter satisfaction are documented byproducts of changes to population demography that occur under QDM (Jacobson 1992, Karns and Ditchkoff 2012), but how demography can affect the fawning season has received limited attention in the literature. It has been suggested that increased male population age structure and a more balanced sex ratio, products of QDM, can alter the timing and duration of the breeding season (Guynn and Hamilton 1986, Jacobson 1992). In iteroparous mammalian species such as white-tailed deer, the timing of breeding season has evolved to allow fawns to be born during peak food availability, which helps ensure that females are able to meet the high nutritional demands of gestation and lactation (Verme 1965, Bronson 1989). In addition, Jacobson (1992) found that breeding chronology shifted 2–3 weeks earlier with an increase in older males that was accomplished by protecting young males from harvest.

An earlier breeding season may be important for mitigating negative effects of late-born fawns. Research in the southeast revealed late born fawns typically have smaller antlers and bodies at age 1.5 than fawns born earlier in the season (Knox et al. 1991,

Gray et al. 2002, Saalfeld and Ditchkoff 2007). Late-born fawns may be at a developmental disadvantage because food availability has passed its peak and nutritional availability relates directly to the amount of milk a female can provide (Verme 1965), in addition to having less time for development prior to winter. Additionally, female fawns born after the peak fawning period do not usually reach puberty their first breeding season (Verme and Ullrey 1984), and male fawns may not develop spermatozoa in time to breed during their first rut (Peles et al. 2000). These studies suggest that birth date has impacts on development of fawns through their first few years.

Whereas timing of the fawning season is certainly important, the duration of the fawning season may be equally significant. Guynn and Hamilton (1986) found that breeding season condensed as adult sex ratio shifted from female biased to being balanced between the sexes. Synchrony of estrus among females during the breeding season may lead to greater survival of fawns the following summer (White et al. 2001) due to the theory of predator swamping (Ims 1990, Whittaker and Lindzey 1999). Natural selection has guided fawning dates to occur during time periods conducive to successfully raising offspring, but restocking white-tailed deer in the southeast has created a mosaic of fawning dates in the region (Gray et al. 2002). Furthermore, the recent colonization of coyotes (*Canis latrans*) to southeastern ecosystems has introduced a different selective pressure to deer in this region. Several studies in the southeast have recognized coyotes as being a key predator negatively impacting fawn recruitment (Saalfeld and Ditchkoff 2007,

Howze et al. 2009, Kilgo et al. 2012, Jackson and Ditchkoff 2013, McCoy et al. 2013, Robinson et al. 2014, Chitwood et al. 2015). Differences in the timing of the breeding season might explain why fawn recruitment is lower in areas of the Southeast, while other regions within the coyote's native range in the western United States do not show similar impacts (Huegel et al. 1985, Brinkman et al. 2004, Grovenburn et al. 2011). The fawning season in the southeast is typically later in the year compared to other areas of the white-tailed deer's range (Haugen 1959, Leuth 1967, Gray et al. 2002) which may exacerbate the negative influence coyotes are having on neonatal survival because coyote pups might be able to hunt by the time fawning occurs (Harrison and Harrison 1984, Harrison et al. 1991, Saalfeld and Ditchkoff 2007). Having fawns born earlier in the growing season may increase fawn survival because coyote pups may lack experience catching prey earlier in the year or because pups have differential hunting tactics compared to older, more dominant coyotes (Gese et al. 1996).

The effects of population demography on fawning season have yet to be clearly established, so our objective was to study effects of population age and sex ratio on the timing and duration of fawning season in central-Alabama during a changing demography. Older (≥ 3.5 years old) males have been documented performing more ritualized breeding behavior (i.e., rubbing, scraping, tending females) than young (1.5-year-old) males (Ozoga and Verme 1985). Thus, we predicted that as male structure became progressively older, average fawning dates would occur earlier as more does would be bred on their first estrus cycle (Guynn and Hamilton 1986, Jacobson 1992). We also predicted that fawning season duration would be more condensed when more mature males were present in the population (Guynn and Hamilton 1986, Miller et al. 1995).

Study Site

Our study site was the 174-ha Auburn Captive Facility (ACF) located in Camp Hill, Alabama. The population consisted of deer that were in the area at the time the fence was constructed in 2007, and their descendants. The perimeter of the ACF was bordered by a 2.6-m deer-proof fence which prevented immigration and emigration. Deer were fed 18% protein pellets ("Deer Feed," South-Fresh Feeds, Demopolis, Alabama) ad libitum year round using three free choice feeders and their diet was supplemented by corn during fall and winter.

The two main cover types inside the ACF were open hayfields (40%) and mixed forest (60%). The predominant grass species found inside the ACF was bermuda grass (*Cynodon* sp.). Other grasses present included fescue (*Festuca* sp.), big bluestem (*Andropogon* sp.), Johnson grass (*Sorghum* sp.), dallisgrass (*Paspalum* sp.),

and bahia grass (*Paspalum* sp.). The forest species were oak (*Quercus* spp.), hickory (*Carya* spp.), maple (*Acer* spp.), and pine (*Pinus* spp.) of varying age. The general habitat within the wooded areas included a thick closed canopy with little understory growth. Forest edges and creek bottoms contained dense understory of Chinese privet (*Ligustrum sinense*). Water was available to deer from several creeks that ran throughout the property. Elevation ranged from 190 to 225 m above sea level. The climate in this region of east-central Alabama was moderately warm with mean high temperatures of 32.5°C in July and mean low temperatures of -0.5°C in January. Average annual precipitation in the area was approximately 131 cm (National Climate Data Center 2013).

Methods

Population estimates were derived using bi-yearly camera surveys at sites baited with shelled corn and along trails (McCoy et al. 2011). Ear tags, freeze brands, and unique antler configurations allowed us to identify individuals and estimate abundance, sex ratio, and age structure of the population. We used camera survey data in conjunction with current capture and mortality records to reconstruct the total population for each year and generate final estimates of demographics.

VITs (M3930, Advanced Telemetry Systems, Isanti, Minnesota) were inserted from 2010 to 2013 in adult female deer beginning mid-February and ending in June using methods described by Saalfeld and Ditchkoff (2007). Females were captured using tranquilizer dart projectors (M193, Pneu-Dart Inc., Williamsport, Pennsylvania) equipped with night vision scopes. We also captured adults with a 0.8-ha modified box trap and used a pole injector for chemical immobilization. Chemical immobilization occurred with an intramuscular injection of Telazol (Fort Dodge Animal Health, Fort Dodge, Iowa; 125 mg ml⁻¹ given at a rate of 4.5 mg kg⁻¹) and xylazine (Lloyd Laboratories, Shenandoah, Iowa; 100 mg ml⁻¹ given at a rate of 2.2 mg kg⁻¹) followed by reversal with Tolazine (Lloyd Laboratories, Shenandoah, Iowa; 100 mg ml⁻¹ given at a rate of 6.6 mg kg⁻¹; Miller et al. 2004). Deer were aged by examining tooth replacement and wear (Severinghaus 1949). Captured deer were marked with uniquely numbered ear tags and freeze brands. VITs were monitored once a week from insertion until 4 July, after which monitoring increased to four times per 24-hour period until the last transmitter had been expelled.

We used temperature sensitive VITs that would double the pulse rate due to the drop in temperature when expelled. Binary codes were programmed into the VITs so that expulsion time could be determined with an accuracy of ± 15 minutes. Upon detecting an expelled transmitter, we used telemetry to home in on the VIT (Carstensen et al. 2003). A thermal imaging camera (Ray-

theon Palm IR 250D, Waltham, Massachusetts) was used to locate fawns not directly at the birth site. In these instances, the location of the VIT was used as a focal point for a grid search. Fawns were handled quickly (<10 min) to prevent any human induced abandonment (Powell et al. 2005). VIT success percentages were calculated by dividing the number of successfully expelled VITs (where a fawn was recovered) by the number of females implanted each year. All capture and handling procedures were in accordance with protocols approved by the Auburn University Institutional Animal Care and Use Committee (PRN numbers: 2008-1417, 2008-1421, 2010-1785, 2011-1971, and 2013-2372) and were in compliance with guidelines adopted by the American Society of Mammalogists Animal Care and Use Committee (Sikes et al. 2011).

Date of birth was recorded for each successful VIT expulsion and was converted to Julian date for statistical analysis. VITs that were expelled during the fawning season but not located at definitive birth sites were not included in analysis as they were assumed to be premature expulsions. We used linear regression in Program R to examine differences in fawning dates dependent on average male age by year (R Core Team 2012). We treated litters as one experimental unit and thus recorded one Julian date per birth site, no matter how many fawns were born. We considered the relationship between male age and fawning date significant at $\alpha \leq 0.05$. We also compared fawning season within the ACF to estimated fawning dates for adult female (≥ 2.5 years old) deer harvested within 40 km of our study site. These data were collected during spring reproductive surveys by the Alabama Department of Conservation and Natural Resources in Tallapoosa County from 1995–2013 using fetal measurements (Hamilton et al. 1985).

Results

Population reconstruction indicated minimum annual herd size ranged from 69 (2008) to 122 (2011) individuals (Table 1). Adult sex ratio over the course of the study ranged from 1.00M:1.04F in 2010 to 1.00M:0.78F in 2012. Approximately 90% of adult deer were captured and marked as part of ongoing research at the study site. The proportion of known-age animals in the population was 81.8% in 2013. Mean adult (>0.5 years old) male age increased from 2.74 in 2010 to 3.92 in 2013 and mean adult female age increased from 3.68 in 2010 to 4.17 in 2013.

A total of 55 females were fitted with VITs from 2010 to 2013, and we recovered 37 neonates from 24 of these females. Successful VIT retention was 58.8 ($n=17$), 30.0 ($n=10$), 50.0 ($n=12$), and 71.4% ($n=7$) in 2010, 2011, 2012, and 2013, respectively. We censored eight VITs from analysis in 2013 because batteries died before parturition occurred. Six VITs were retained nearly to parturition but were not included in fawning date analysis because we

were unable to locate a birth site. Seventeen VITs were prematurely expelled before fawning season. Mean ages of implanted females were 3.7 ($n=17$), 1.8 ($n=10$), 3.2 ($n=12$), and 5.7 ($n=7$) years of age in 2010, 2011, 2012, and 2013, respectively. Two females were implanted with VITs in multiple years, one of which was implanted for three consecutive years with no apparent adverse effects on reproduction as she gave birth to five fawns over that span.

For every one year increase in average age of males, fawning date occurred 13.1 days earlier ($t=-3.12$, $df=21$, $P=0.014$). The length of fawning season ranged from 31 (Julian date 210 to 241; 29 July to 29 August) days in 2010 to 25 (208 to 233; 27 July to 21 August) days in 2011, but this difference was not significant ($t=0.19$, $P=0.895$). Mean fawning dates were 12 August \pm 3.11 days ($\bar{x} \pm SE$), 10 August \pm 7.45 days, 2 August \pm 4.02 days, and 30 July \pm 5.83 days for 2010, 2011, 2012, and 2013, respectively (Figure 1). Mean fawning date did not differ from that of wild Alabama deer harvested in 2013 within 40 km of the ACF ($t=-0.44$, $P=0.663$).

Table 1. Known white-tailed deer breeding populations by sex, age class, and cohort birth year from 2008–2013, Auburn Captive Facility, Camp Hill, Alabama.

Age	2008	2009	2010	2011	2012	2013
Total popln. ^a	69 (35 ^b)	84 (51 ^b)	98 (63 ^b)	122 (90 ^b)	114 (89 ^b)	110 (90 ^b)
Males	25 (15)	40 (29)	48 (34)	62 (50)	64 (53)	53 (45)
0.5	11 (9)	16 (15)	14 (11)	21 (21)	13 (13)	8 (8)
1.5	8 (6)	10 (8)	13 (12)	11 (8)	12 (12)	9 (9)
2.5	3 (0)	8 (6)	9 (7)	12 (11)	11 (8)	6 (6)
3.5	3 (0)	3 (0)	6 (4)	8 (6)	11 (10)	9 (6)
4.5	0	3 (0)	3 (0)	6 (4)	8 (6)	8 (8)
5.5	0	0	3 (0)	2 (0)	6 (4)	7 (5)
6.5	0	0	0	2 (0)	2 (0)	4 (3)
7.5	0	0	0	0	1 (0)	1 (0)
8.5	0	0	0	0	0	1 (0)
Females	44 (20)	44 (22)	50 (29)	60 (40)	50 (36)	48 (36)
0.5	16 (11)	7 (6)	13 (10)	12 (12)	9 (9)	6 (6)
1.5	7 (6)	14 (9)	5 (4)	13 (10)	10 (10)	9 (9)
2.5	8 (3)	5 (4)	13 (8)	5 (4)	8 (5)	8 (8)
3.5	7 (0)	7 (3)	5 (4)	12 (7)	3 (3)	5 (2)
4.5	4 (0)	5 (0)	6 (3)	5 (4)	9 (4)	3 (3)
5.5	1 (0)	4 (0)	4 (0)	6 (3)	4 (3)	8 (4)
6.5	0	1 (0)	2 (0)	3 (0)	5 (2)	4 (3)
7.5	1 (0)	0	1 (0)	2 (0)	1 (0)	3 (1)
8.5	0	1 (0)	0	1 (0)	1 (0)	1 (0)
9.5	0	0	1 (0)	0	0	1 (0)
10.5	0	0	0	1 (0)	0	0
Sex Ratio						
(M:F) ^c	1:2.0	1:1.5	1:1.1	1:1.2	1:0.8	1:0.9

a. Abundances estimated using combination of camera surveys, field observations, capture of live animals, and recovery of deceased animals. All estimating methods indicated $\geq 90\%$ of animals in population were marked during the study yielding largely known population sizes.

b. Number of individuals initially captured at ≤ 2.5 years old.

c. For animals >0.5 years old.

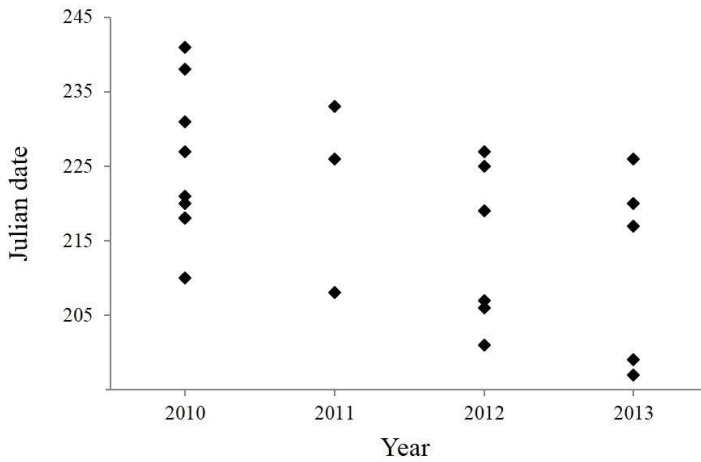


Figure 1. Julian birth dates of white-tailed deer fawns captured from 2010–2013 using vaginal implant transmitters at the Auburn Captive Facility, Camp Hill, Alabama.

Discussion

We documented an earlier fawning season as male population demography changed. Even with a low sample size, our significant results suggest that male population demographics influenced the timing of parturition. Jacobson (1992) documented a similar shift toward earlier breeding when QDM harvest strategies increased male age structure. Our population mimicked the changes managers would expect under QDM as male age structure increased over time.

Sex ratio remained relatively constant over the course of our study, which differed from what Guynn and Hamilton (1986) documented as adult sex ratio shifted from female biased to being balanced between the sexes. Having more mature males relative to females in a population increases sexual competition and leaves fewer females not bred after their first estrous cycle (Ozoga and Verme 1985, Miller et al. 1995), but sex ratios close to parity or slightly skewed toward females seem to function similarly. From 2010 to 2013, our population never had an estimated sex ratio less than 1.00 male for every 1.04 females, so we may not have been able to detect a condensed fawning season because sex ratios were already balanced when we began using VITs to document the fawning season. Similarly, Kilgo et al. (2012) found that fawning season at the Savannah River Site in South Carolina still occurred over a 2.5-month period, even when adult sex ratio approached parity for more than 40 years. Although speculative, we believe the fawning season may have condensed since 2007 when the research facility was established, but we have no data on fawning season duration before VITs were utilized beginning in 2010.

Whether it is age structure or adult sex ratio affecting the fawning season, there is little doubt that late-born fawns are at a disad-

vantage relative to more earlier born from their cohort (Gray et al. 2002). Late born female fawns usually do not breed, or if they do, they breed late in the breeding season which perpetuates the late-born fawn cycle. Evidence suggests negative effects of late born fawns, such as small body size and reduced fecundity, may even persist into adulthood (Clutton-Brock et al. 1982, Mech et al. 1991, Schmidt et al. 2001, Monteith et al. 2009), which potentially limits lifetime breeding success. Ongoing research at our study site will monitor lifetime breeding success of late born fawns. Although our population did not experience winter mortality, another disadvantage late born fawns incur is increased risk of winter mortality, especially in northern regions where winter climates are severe (Delgiudice et al. 2006, Carstensen et al. 2009).

Despite the occurrence of coyotes at our study site, we failed to document any reduction in fawn recruitment. The timing of the fawning season is important as the relatively recent colonization of coyotes to southern regions is a concern to managers having to deal with reduced fawn survival. Although information is lacking for coyotes in the southeast, they have been well studied within their native range (Hilton 1978). Coyote pups are born in early spring and usually do not leave the vicinity of their den sites until 6–8 weeks old (Harrison and Gilbert 1985). Selective pressures to have fawns born during a specific time period may become more pronounced as coyotes continue to persist on the southeastern landscape. In areas where coyotes are negatively impacting fawn recruitment, harvest recommendations that influence deer population structure could mitigate some of these impacts (Kilgo et al. 2012, Robinson et al. 2014, Chitwood et al. 2015).

Although having fawns born earlier and over a shorter time period may increase survival and development of fawns (Jacobson 1992), there may be potential negative consequences found in populations that have increased proportions of mature males. The intense competition found in these populations can lead to elevated levels of injury and stress in males. In a population with a large proportion (>50%) of mature males (≥ 3.5 years old), Ditchkoff et al. (2001) reported mortality of mature males due to rut-related stress and physical exertion was greater than human-induced hunting mortality. Ozoga and Verme (1985) observed evidence of behavioral differences in breeding activity between old (≥ 3.5 year olds) and young (1.5 year olds) males by manipulating male age structure within the population. When only 1.5-year-old males were present, they observed fewer rubs and scrapes than when only older males were present, but no differences in adult male survival were reported. Another potential consequence of managing populations for increased numbers of older males is increased risk of intracranial abscessation, which is thought to be caused by breeding activities such as antler sparring, rubbing, or antler casting (Davidson

et al. 1990). It has been reported that intracranial abscessation can be a significant cause of mortality in older males (Davidson et al. 1990, Karns et al. 2009, Cohen et al. 2015). Antler breakage patterns are also of management importance as they may be indicative of a population with a high proportion of mature males (Karns and Ditchkoff 2012). Although we did not collect data on antler breakage, anecdotal evidence suggests more breakage occurred in 2013 than in 2010, which also suggests that competition for females in the ACF was more intense in 2013 compared to 2010.

Although male demographics are certainly important, female nutrition and age also play an important role as to when an individual will enter estrus (Abler et al. 1976) and give birth (Verme 1969). Gestation may be extended for females in poor condition while females in good condition may not gestate as long (Verme 1965). We did not collect data on native forage availability during our study but the nutritional plane (due to supplemental feed provided ad libitum) was relatively constant throughout the study. The age of females fitted with VITs was consistent throughout the study to isolate the effect of female demographics on fawning date. Guynn and Hamilton (1986) found that female age was not an important determinant of when breeding occurred.

Managers seeking to improve fawn survival as well as allow more time to develop prior to winter may consider increasing male age structure, which increases breeding competition and results in earlier fawning. Earlier-born fawns get a head start on development which may persist into adulthood. The positive effects of earlier fawning may not be apparent the first season QDM is implemented, but benefits should continue to accrue into successive years of the management program as early born fawns reach maturity. In addition to the positive impacts on fawn development, an earlier fawning season may also help managers seeking to counteract reduced fawn survival caused by coyote predation (Kilgo et al. 2012, Robinson et al. 2014, Chitwood et al. 2015).

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