Research Article

Effect of Male Age Structure on Reproduction in White-Tailed Deer

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ABSTRACT Selective harvest regimes that create female-biased sex ratios can potentially lead to delayed breeding, reduced breeding synchrony, reduced productivity, and a female-biased sex ratio of offspring. These resulting changes in breeding behavior and population dynamics have potential to adversely affect population growth. In 2002, Pennsylvania implemented harvest regulation changes that reduced deer density (increased harvest of antlerless deer) and increased the number and age of antlered deer (implemented antler point restriction regulations) that resulted in a less female-biased sex ratio. We monitored date of conception, productivity (embryos/female), and sex ratio of embryos during 1999–2006 to test if timing of breeding occurred earlier and with greater synchrony, if productivity of females increased, and if the sex ratio of offspring would shift towards more males. Deer density decreased 23% and the adult ($\geq$1.5 yr old) sex ratio declined from 2.30 to 1.95 females/male. The ratio of $\geq$2.5-year-old to 1.5-year-old males shifted towards more older males (1:3.7 in 2002 to 1:1.59 in 2006) and the $\geq$2.5-year-old male population increased from 41,853 during 1999–2001 to 54,064 by 2006. We found no evidence of any change in the timing or variability of date of conception, productivity, or offspring sex ratio. We conclude that harvest regulation changes implemented in Pennsylvania, USA, were insufficient to affect timing of breeding or population dynamics and that efforts by managers to identify a desired sex ratio or manipulate sex ratios to achieve management goals on a statewide scale will be challenging. © 2019 The Wildlife Society.

KEY WORDS age ratio, antler point restrictions, breeding, *Odocoileus virginianus*, productivity, selective harvest, sex ratio, white-tailed deer.

In ungulate species, selective harvesting that results in a female-biased sex ratio and younger age structure can reduce fecundity, alter breeding dates, reduce birth synchrony, result in fewer male offspring, and reduce offspring body mass (Milner et al. 2007). Furthermore, male-biased harvest management strategies have raised concerns about selective effects on life-history evolution (Festa-Bianchet 2003, Mysterud 2011) and loss of genetic variability (Ryman et al. 1981). Mysterud et al. (2002) argued that the effects of males on population dynamics may be non-trivial and they identified several potential mechanisms that could affect timing of breeding that, in turn, could affect neonate survival and fertility of females.

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White-tailed deer (*Odocoileus virginianus*) populations throughout North America have endured harvest rates as high as 80% of antlered males (Adams and Hamilton 2011). In Pennsylvania, USA, throughout the twentieth century, hunting regulations for white-tailed deer resulted in a female-biased sex ratio but with no adverse effect on overall abundance (Diefenbach et al. 1997). During 1981–2001, the annual harvest rate of antlered deer was 0.77–0.84 and few male deer survived >3.5 years of age (Wallingford et al. 2017). In 2002, Pennsylvania implemented harvest regulations that increased the survival rate of males and reduced the survival rate of females by implementing antler point restriction (APR) regulations for males and increased allocation of antlerless licenses to harvest females (Wallingford et al. 2017). Pennsylvania's deer population has adversely affected forest plant communities and agricultural crops and the Pennsylvania Game Commission (PGC) was unable to balance deer densities with habitat conditions (Diefenbach et al. 1997). The implementation of APRs was designed to maintain hunter satisfaction with more older deer harvested despite lower deer densities from

increased antlerless harvests. The changes in harvest regulations implemented in 2002 created an older age structure in the male population, reduced the overall population density, and created a more balanced adult sex ratio (Wallingford et al. 2017). Although Pennsylvania's management objectives for APRs were not to induce changes in the breeding behavior of white-tailed deer (Wallingford et al. 2017), this large-scale manipulation with changes in the sex-age structure of a white-tailed deer population could affect timing of births, productivity (embryos/females), and sex ratio of offspring following a shift to an older male age structure, a more balanced adult sex ratio, and reduced population density.

In ungulates, a skewed adult sex ratio biased toward females and a younger male age structure tends to reduce breeding synchrony and delay birth dates, which leads to lower offspring survival (Mysterud et al. 2002, Milner et al. 2007). Early behavioral research in white-tailed deer suggested that older-aged males dominate breeding behavior and have greater mating success (Hirth 1977, Marchinton and Hirth 1984). Subordinate males were presumed to do little breeding and potentially disrupt the social order of the population by harassing matriarchal females (Townsend and Bailey 1981; Ozoga and Verme 1982, 1985). Furthermore, the presence of males can induce estrus in white-tailed deer (Verme et al. 1987) and older males contain greater concentrations of volatile compounds in their urine, which may convey their social status (Miller et al. 1998). Consequently, the potential mechanism by which breeding could occur earlier and with greater synchrony would be that the presence of more older males would lead to more efficient breeding (because a more structured social order of dominance would exist) and more females would be bred during their first estrus. Ozoga and Verme (1985) manipulated the age structure of males in a captive herd and reported that breeding was most variable in older females (>3.5 yr old) bred by 1.5-year-old males.

In an experimental manipulation of the male age structure of a white-tailed deer population maintained in an enclosure, Ozoga and Verme (1985) reported no short-term deleterious effects on fecundity rates in a population with only 1.5-year-old males. Recent research on paternity in white-tailed deer indicates age structure has little effect on breeding opportunities for males because subadult males (1.5–2.5 yr old) sired offspring even when mature males were present (Sorin 2004, DeYoung et al. 2009). Under a deer management strategy where objectives were to balance the sex ratio and sustain an older age structure of males, Turner et al. (2016) reported that 1.5- and 2.5-year-old males sired 59% of offspring when >50% of the population was estimated to be ≥3.5 years old. However, when ≥30% of the male population was ≥3.5 years old, DeYoung et al. (2009) and Sorin (2004) reported that 1.5-year-old males sired a smaller proportion of offspring compared to their relative abundance in the population. In a population where 80% of males were <3.5 years old, the siring of offspring was nearly proportional to the age structure of the male population (DeYoung et al. 2009). These studies collectively conclude that 1.5-year-old males contribute to a large proportion of the breeding even when 50%–80% of the population consists of males >3.5 years old; this indicates that white-tailed deer productivity may not be affected by harvest strategies that result in a female-biased sex ratio and younger male age structure.

Productivity could increase in response to a change in harvest strategies if productivity is density dependent, whereby reduced deer density resulted in improved habitat quality and increased available *per capita* food resources. A decrease in the density of the deer population might result in an increased availability of food resources and thus improved body condition of females. The proportion of fawns that became pregnant is a sensitive measure of a population's level of nutrition because body mass of female fawns by the breeding season determines their ability to breed (Gaillard et al. 2000, DeYoung 2011). Thus, a change in the proportion of fawns bred, and no change in productivity of older females, would be the expected response to a change in deer density rather than a response to changes in the sex-age structure of the population.

Females with good nutrition have been shown to produce more males; thus, more male offspring will be produced if a density-dependent relationship with body condition exists (Trivers and Willard 1973, Clutton-Brock et al. 1984, Wauters et al. 1995, Kohlmann 1999). However, other factors potentially could influence offspring sex ratio. Ozoga and Verme (1985) reported a greater proportion of males were sired by older males, although results were not statistically significant. In an experimental manipulation, Sæther et al. (2004) reported that a younger age structure in male moose (*Alces alces*) resulted in a lower proportion of male offspring born, although manipulation of the sex ratio had no effect.

Our objective was to test several hypotheses about how increasing the number and proportion of older males in the population and reducing overall deer density would affect breeding behavior. More older males in the population are hypothesized to increase breeding synchrony; therefore, we predicted that the older age structure of males would lead to an earlier average date of breeding and smaller standard deviation in breeding dates. We predicted no change in the productivity of adult females because previous research has shown that even 1.5-year-old males contribute significantly to breeding in white-tailed deer. Reduced deer density and more older males is hypothesized to result in more male offspring produced. We predicted that offspring sex ratios would shift towards more males as the adult sex ratio became less female biased and population density declined. To test our predictions, we collected data on pregnancy rates (proportion of females pregnant), conception dates, productivity (embryos/female), and embryo sex ratios by examining a sample of road-killed females before (1999–2002) and after (2003–2006) Pennsylvania implemented APR regulations and increased antlerless harvests.

STUDY AREA

Pennsylvania, located in the mid-Atlantic region, was 119,282 km^2 and approximately 60% forested of primarily northern hardwoods or oak (*Quercus* spp.)–hickory (*Carya* spp.) forest types (Cuff et al. 1989). Non-forested lands were used for agriculture, primarily row crops, and human development, or were reclaimed surface mines (Cuff et al. 1989). The white-tailed deer population in Pennsylvania increased in distribution and abundance through the twentieth century (Diefenbach et al. 1997), which affected the species richness and diversity of forest plant and animal communities (Horsley et al. 2003, Nuttle et al. 2011). Mean annual temperature was 15 °C in the southeastern part of the state near sea level and 8 °C in the higher elevations of the north-central plateaus (<979 m above sea level). Precipitation was evenly distributed throughout the year and averaged 86–132 cm and average annual snowfall varied from 50 cm to 228 cm, depending on region of the state (http://climate.met.psu.edu/data/state/, accessed 4 Dec 2018).

The PGC delineated the state into management units based on natural and man-made physical features, such as state numbered roads, federal highways, and rivers. Management units had similar land use, human density, and land ownership (public vs. private). During our study (2002–2009), the PGC was transitioning from using political boundaries (counties) to management units that delineated relatively homogeneous areas with readily identifiable boundaries for hunters. Consequently, the reproduction data (see Methods) were collected based on 18 Deer Management Units (DMUs), but harvest data and population estimates were based on 22 Wildlife Management Units (WMUs) formally adopted by the Board of Commissioners (Fig. 1). Both types of management units delineated similar areas of Pennsylvania. Deer population abundance was monitored by WMU and was manipulated by regulating number of WMU-specific antlerless licenses issued (Rosenberry et al. 2011).

METHODS

Treatment: Change in Sex-Age Population Structure

Prior to 2002, purchase of a general hunting license allowed a hunter to harvest 1 antlered deer/year. The number of available hunting licenses for antlerless deer was allocated by WMU and issued on a first-come, first-served basis. Antlerless licenses were limited to 2 antlerless licenses/hunter/WMU, except in some WMUs surrounding Pittsburgh and Philadelphia (2B, 5C, and 5D; Fig. 1) where the number of licenses per hunter was not limited. The definition of an antlered male legal for harvest was any animal with 1 antler >7.5 cm long or any length branched antler. Under these harvest regulations, the average statewide harvest rate for antlered deer during 1981–2001 was 0.81 (Wallingford et al. 2017).

In 2002, APR harvest regulations for males were enacted and antlered males legal for harvest had 1 antler with ≥3 or ≥4 points depending on the WMU, except WMUs 2B, 5C, and 5D. A point was defined as any tine ≥2.5 cm long and a brow tine of any length, but in 2003 all antler points

had to be ≥2.5 cm long and WMUs 2B, 5C, and 5D were included in these APR regulations. The objective of APRs was to increase the number of older-aged males in the population (Wallingford et al. 2017).

In addition to increasing the antlered population, the overall population of deer was reduced by increasing antlerless harvests (Table 1). We estimated harvests using the method described by Rosenberry et al. (2004). We estimated deer population size for each WMU using a sex-age-kill model modified for use with a population under APR regulations (Norton et al. 2013). Using model results, we estimated population size of subadult (1.5 yr old) and adult (≥2.5 yr old) male and ≥1.5-year-old female deer to document changes in the sex-age structure from 2002 to 2009. The population estimates used to derive sex and age ratios represented population sex-age structures during the breeding season.

Data Collection and Analysis

We examined female deer killed by various causes, primarily road-killed deer, from 1 February–31 May during 2000–2007 (representing the 1999–2006 breeding seasons). No live animals were handled, and we provided protective equipment to field personnel. We checked the uterus of each female to determine reproductive status, and if pregnant we determined sex and measured crown-rump length of each embryo. We used average crown-rump length in the relationship between age and crown-rump length to estimate date of conception (Hamilton et al. 1985) if multiple embryos were present. Also, we recorded the DMU in which the adult female died and collected 1 side of the lower jaw to age according to tooth wear and replacement into 3 age categories: <1 year old (fawn), 1 year old (subadult), and ≥2 years old (adult; Severinghaus 1949), assuming a birth date of 1 June. We excluded data from DMUs 7 and 18 (areas surrounding Philadelphia and Pittsburgh) because the timing of the implementation of APRs was delayed by 1 year compared to other DMUs.

To investigate whether changes in sex-age structure of the population affected timing of conception, we used a
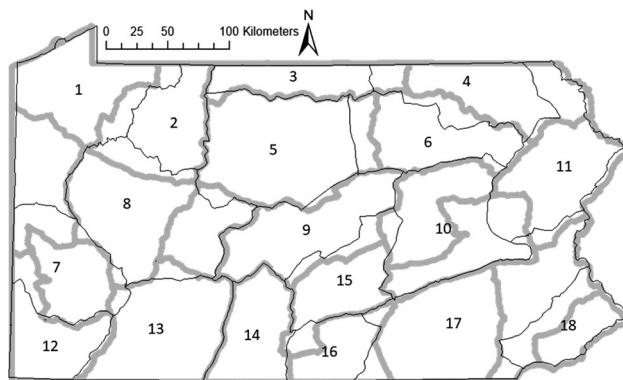

Figure 1. White-tailed deer management units (1–18; solid line) used when collecting embryo data from road-killed females and wildlife management units (outlined in gray) used when collecting data from hunter harvested deer, Pennsylvania, USA, 1999–2009. We excluded units 7 (Pittsburgh and suburbs) and 18 (Philadelphia and suburbs) from analyses.

Table 1. Pre-hunt population size, antlerless harvest, antlered harvest (subadult = 1.5 yr old; adult = ≥2.5 yr old), Pennsylvania, USA, 1999–2006. Beginning in 2002 antler point restriction regulations were implemented that reduced the proportion of subadult deer legal for harvest.

| Year | Pre-hunt population | Antlerless harvest | | Antlered harvest | | | | | |
		Estimate	SE	Total[a]	SE	Subadult	SE	Adult	SE
1999	1,364,688	201,519	1,708	207,644	1,738	165,600	1,521	41,853	403
2000	1,487,898	298,036	1,803	241,397	2,433	198,585	2,135	42,579	416
2001	1,372,594	272,629	1,718	198,832	1,834	157,089	1,597	41,619	393
2002	1,380,479	298,791	1,487	161,949	1,987	112,019	1,586	49,832	930
2003	1,254,997	334,154	2,256	140,987	1,788	81,507	1,278	59,340	987
2004	1,174,230	284,158	2,057	124,107	1,596	59,323	990	56,873	942
2005	1,140,321	234,608	1,999	120,080	1,760	63,251	1,152	56,864	1,046
2006	1,134,760	227,135	1,988	125,634	1,656	71,474	1,148	54,064	941

[a] Includes deer reported as harvested in which the wildlife management unit was unknown and not corrected for hunter reporting rate (≤0.33% of report cards received).

Bayesian approach with a hierarchical model of the timing and variance of date of conception. We allowed conception date to vary among DMUs, year, and DMUs within years (i.e., a DMU × year interaction; a variance component model). Also, we allowed the residual standard deviation to vary among years and used this model as a null model because it did not model any change in year-specific standard deviations in conception dates. We conducted analyses separately for each age class (fawn, subadult, adult) because male age structure might have a differential effect on timing of conception in each age class (Ozoga and Verme 1985).

The form of the hierarchical model was:

$$y_{ijk} \sim N(\beta_0 + \alpha_{j(i)} + \beta_{k(i)} + \gamma_{j,k(i)}, \sigma_k^2), \quad \text{for } i = 1, \ldots n_{jk}$$
$$\alpha_j \sim N(0, \sigma_\alpha^2)$$
$$\beta_k \sim N(0, \sigma_\beta^2) \quad (1)$$
$$\gamma_{j,k} \sim N(0, \sigma_\gamma^2)$$
$$\log(\sigma_k) \sim N(\mu_\sigma, \omega_\sigma^2), \quad \text{for } k = 1, \ldots K$$

where y_{ijk} was calendar date of conception for observation i in WMU j and year k; α_j was the WMU random effect and β_k was the random effect for year k; $\gamma_{j,k}$ was the WMU × year random effect. The random effects α_j, β_k, and $\gamma_{j,k}$ were assumed independent and identically distributed as (N, σ_x^2). We assumed a normal population distribution for log$_e$-transformed σ_j (year-specific SDs), with mean μ_σ and variance ω_σ^2. We used non-informative normal priors for all parameters.

To test whether standard deviations of conception date declined after APRs were implemented, we fitted 2 models with predictor variables to model the standard deviation among years. We modified equation (1):

$$\log(\sigma_k) \sim N(\delta_0 + \delta_1 \times treatment_k, \omega_\sigma^2), \quad \text{for } k$$
$$= 1, \ldots K \quad (2)$$

where δ_0 and δ_1 were intercept and slope, respectively. Treatment represented 2 different matrices of dummy variables to model how variance changed over time. In the first model, the standard deviation simply differed

before and after APRs were implemented, where in the 8 × 1 matrix treatment, treatment = 0 before APRs and treatment = 1 after APRs were implemented. Because date of conception might shift over time, in a second model we estimated a different standard deviation the first year after APRs were implemented and a different but constant standard deviation in all following years (in this model we modified eq. 2 to include a second slope parameter, δ_2, to be estimated corresponding to the 8 × 2 matrix treatment).

We examined 95% credible intervals (CRIs) to determine significance of predictor variables (whether 95% CRIs overlapped zero). We fitted these Bayesian models using a Markov chain Monte Carlo algorithm implemented in JAGS (4.2.0; Plummer 2011) accessed via R statistical software (R version 3.5.1, www.r-project.org, accessed 30 Aug 2018) with the R2jags package (Su and Yajima 2015). We ran 3 parallel chains with different initial values and after discarding the first 50,000 samples, we retained every third sample for 45,000 samples. To assess convergence for each parameter, we examined the scale reduction factor ($\hat{R}$), trace plots, and plots of posterior distributions.

To investigate whether productivity (embryos/female) increased, we analyzed the number of embryos (0–4) produced by subadult and adult females. We used a linear mixed-effect model

$$y_{ijk} \sim Poisson(\beta_0 + \delta_1 + \delta_2 + \alpha_{j(i)}), \quad \text{for } i = 1, \ldots n$$
$$\alpha_j \sim N(0, \sigma_\alpha^2)$$

where y_{ijk} was number of embryos for observation i in WMU j and year k, α_j was the WMU random effect, δ_1 was an indicator variable of prior to APRs creating an older age structure (1 if year <2003; 0 otherwise), and δ_2 was an indicator variable for the first year APRs had an effect (1 if year = 2003; 0 otherwise). The WMU random effect, α_j, was assumed independent and identically distributed as (N, σ_x^2). We implemented these models in the R statistical software with the glmer function in package arm (Gelman et al. 2018) in R. All models included the WMU random effect, but we compared an intercept-only model with models that included only δ_1 and both δ_1 and δ_2. We

selected the model with the lowest Akaike's Information Criterion (AIC) value (Burnham and Anderson 2002).

Our data indicated few fawns were pregnant (<25%) and most had singletons so for productivity analysis of the fawn age group, we analyzed pregnancy rate. We used the same mixed-effects model structure used for the analysis of the number of embryos except the response variable, y_{ij}, was 1 if pregnant and 0 otherwise and we used a binomial (logit) link function. We used the lowest AIC value to select the best model.

To investigate changes in the sex ratio of offspring, we used the same mixed-effects model structure we used for pregnancy rates of fawns. The response variable was sex of fawn (1 = male, 0 = female).

RESULTS

The statewide deer population peaked in 2000 at nearly 1.5 million deer and declined to 1.1 million deer by 2006 (Table 1) as a result of increased antlerless harvests beginning in 2000. The increased antlerless harvests caused a decline in the adult sex ratio (subadult and adult female:antlered male) from 2.30 ± 0.701 (SE) in 2002 to 1.95 ± 0.671 in 2006. Despite the overall population reduction, the number of adult antlered deer harvested increased from 41,853 during 1999 to 54,064 by 2006. The ratio of adult:subadult males in the antlered population declined from $1:3.70 \pm 0.432$ in 2002 to $1:1.59 \pm 0.161$ in 2006 (Table 2; Fig. 2).

We examined 2,209 adult females, 1,397 subadult females, and 2,647 fawns for embryos and calculated date of conception for 3,107 female deer (207–523 per year). Pregnancy rates for fawns ranged from 13% to 24% during 1999–2006 and varied greatly among DMUs (3–38%). Pregnancy rates of subadult and adult deer ranged from 83% to 92% during 1999–2006 with similar variation among DMUs (83–94%). During 1999–2006, the average number of embryos per female ranged from 0.14 ± 0.027 to 0.31 ± 0.039 for fawns, 1.28 ± 0.086 to 1.60 ± 0.068 for subadults, and 1.52 ± 0.046 to 1.69 ± 0.045 for adults.

None of the models of date of conception had year × WMU interactions ($\gamma_{j,k}$) that differed from zero, so we removed that term from models for all age classes. The average date of conception varied among WMUs and years by <5 days, most estimates were not different from zero, with no evidence that mean date of conception was spatially correlated and earlier after APRs were implemented (Fig. 3). For subadults and adults, the parameters that modeled a change in the standard deviation of date of conception over time (δ_1 and δ_2; eq. 2) were not different from zero (Fig. 4). For fawns, δ_1 and δ_2 differed from zero, but the standard deviation of the conception date increased in 2003 (SD = 45.30, 95% CRI = 30.0–69.6) and declined during 2004–2006 (SD = 22.99, 95% CRI = 19.6–26.6) but exceeded the variability during 1999–2004 (SD = 21.87, 95% CRI = 19.24–25.1). We concluded that changes in density and the sex-age structure of the population had no effect on timing of breeding.

We found no evidence that productivity (embryos/female) increased for subadult and adult females after APRs were implemented. The best model for both subadult and adult

Table 2. Average ratios of adult (>2.5 yr old) to subadult (1.5 yr old) antlered males and antlered male (≥1.5 yr old) to adult female (≥1.5 yr old) white-tailed deer among 19 wildlife management units, Pennsylvania, USA, 2002–2009.

Year	Adult male:subadult male			Antlered male:adult female		
	Ratio	SE	95% CI	Ratio	SE	95% CI
2002	1:3.70	0.432	2.85–4.54	1:2.30	0.701	0.92–3.67
2003	1:2.14	0.262	1.63–2.66	1:2.03	0.677	0.70–3.35
2004	1:1.70	0.181	1.35–2.06	1:2.02	0.678	0.69–3.34
2005	1:1.79	0.154	1.49–2.10	1:1.99	0.674	0.67–3.32
2006	1:2.12	0.208	1.71–2.52	1:2.03	0.674	0.70–3.35
2007	1:2.13	0.178	1.78–2.48	1:1.96	0.671	0.65–3.28
2008	1:1.74	0.178	1.39–2.09	1:1.96	0.669	0.65–3.27
2009	1:1.59	0.161	1.28–1.91	1:1.95	0.671	0.64–3.27

productivity indicated productivity was greater before APRs were implemented (subadults: 1.51 ± 0.053 embryos/female; adults: 1.65 ± 0.043 embryos/female) and declined to 1.39 ± 0.046 embryos/subadult female and 1.56 ± 0.030 embryos/adult female (Table 3). Also, we found no evidence that pregnancy rates for female fawns increased. The best model for fawn females estimated different pregnancy rates for 1999–2002 (0.173 ± 0.027), 2003 (0.102 ± 0.032), and 2004–2006 (0.174 ± 0.031; Table 3). Pregnancy rates for fawns and productivity of subadults were lowest in 2003, which coincided with above-average snowfall in central Pennsylvania (https://www.weather.gov/ctp/snowNormals, accessed 27 Jun 2018).

We concluded the sex ratio of embryos did not change during 1999–2006 because for both subadult and adult females, the best model was an intercept-only model (Table 3; Fig. 5). Embryos from subadult females averaged 1.13 ± 0.093 males per female and embryos from adult females averaged 1.09 ± 0.031 males per female.

DISCUSSION

Selective harvest of males can delay birth dates, reduce birth synchrony, delay body mass development, and alter
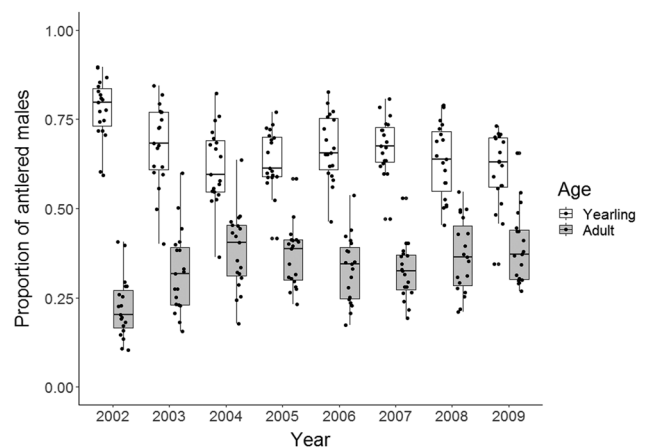

Figure 2. Proportion of subadult (1.5 yr old) and adult (≥2.5 yr old) antlered deer in the population estimated using a sex-age-kill model for 19 wildlife management units (WMU), Pennsylvania, USA, 2002–2009. Each dot represents a WMU, the box represents the median and 25th and 75th quartiles, and whiskers are ±1.5 × inter-quartile range.
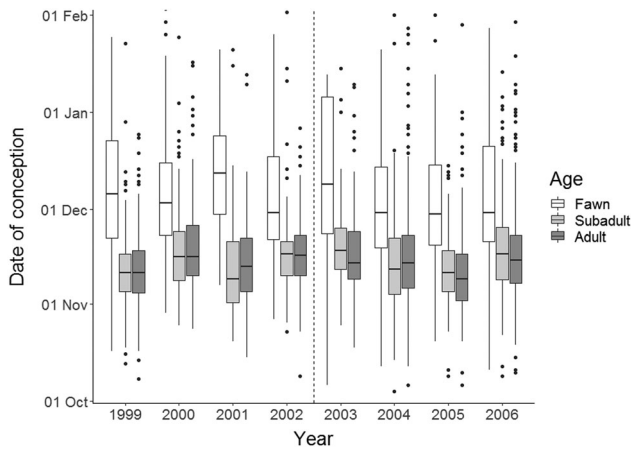
Figure 3. Box (median and 25th and 75th quartile) and whisker ($\pm 1.5 \times$ inter-quartile range) plots for date of conception by age and year for female white-tailed deer, Pennsylvania, USA, 1999–2006. The vertical line indicates the year after antler point restriction regulations were implemented and potentially could have affected conception date.

offspring sex ratios in a number of ungulate species (Milner et al. 2007). In our study, a shift toward older age structure of males stabilized within 2 years of implementation of APRs (Fig. 2), indicating both statistical models used to estimate changes in the standard deviation of conception dates were reasonable (eq. 2). However, we did not detect any changes in timing or synchrony of breeding (Figs. 3 and 4).

There are likely multiple reasons that would explain why changes in the age structure of a male white-tailed deer population would have limited effects on timing and synchrony of breeding. Foremost, breeding is not dominated by older age classes (Sorin 2004, DeYoung et al. 2009). DeYoung et al. (2009) studied 3 populations where the proportion of ≥ 3.5-year-old males was 37–57%, yet 1.5- and 2.5-year-old males sired 30–33% of offspring. In our study the proportion of ≥ 3.5-year-old males in the

population increased from approximately <4% to 11% as harvest rates of ≥ 2.5-year-old males declined from 0.81 to 0.59 (Wallingford et al. 2017). Consequently, if the mechanism by which earlier and synchronous breeding occurs requires older males to dominate breeding, it is unlikely that the age structure changes that occurred in Pennsylvania's deer population resulted in substantially fewer 1.5- or 2.5-year-old males breeding.

There may be limited flexibility regarding when breeding can occur in Pennsylvania, which could also explain why changes in male age structure may have a limited effect on timing of breeding. The timing of breeding should result in an optimal birth date for fawns such that it is not too early that they are exposed to environmental conditions that elevate the risk of mortality (e.g., cold temperatures) yet early enough to attain a body condition in autumn that maximizes winter survival. Synchrony of breeding declines with latitude, but timing of breeding is similar across a large proportion of the white-tailed deer range in North America, and Pennsylvania is located within this region (Diefenbach and Shea 2011).

Jacobson (1992) suggested that the median date of breeding shifted earlier when the mature male:female ratio increased as a result of harvest restrictions on males and increasing antlerless deer harvests. The primary manipulation in that study, however, was a reduced deer density and shift in timing of breeding could have been the result of improved body condition of females. Also, older females have greater pregnancy rates and larger litters and the number of ≥ 2.5-year-old females harvested increased from 62% to 87% of the sample (Jacobson 1992). Jacobson (1992) reported increases in eviscerated body mass, antler beam diameter, and antler beam length. We did not directly measure body condition, but we have no indication that the population reduction caused any increase in reproductive output. Number of embryos per adult female did not change and the percentage of fawns bred varied greatly among DMUs (3–38%) but did not change over time. We would have expected the proportion of fawns bred to increase if body condition improved (Verme 1969), especially because <15% of fawns were pregnant in 8 of 15 DMUs.

The productivity of ungulate populations have been adversely affected by skewed breeding-age sex ratios when the male:female sex ratio was 1:40 in saiga antelope (*Saiga tatarica*; Milner-Gulland et al. 2003) and 1:13 in caribou (*Rangifer tarandus*; Bergerud 1974). In white-tailed deer, it is difficult to achieve a breeding age (≥ 1.5 yr old) male: female sex ratio skewed beyond 1:4 unless adult male annual mortality rates exceed 0.90 and adult female annual mortality rates are <0.2. White et al. (2001) did not detect a relationship between adult sex ratios and productivity in mule deer (*Odocoileus hemionus*) and elk (*Cervus canadensis*). Given the relatively small change in adult sex and age ratios created during our study (Table 2) compared to Milner-Gulland et al. (2003) and Bergerud (1974), it is unlikely those changes would increase productivity.

Ozoga and Verme (1985) reported a trend for older white-tailed deer males to produce more male offspring and
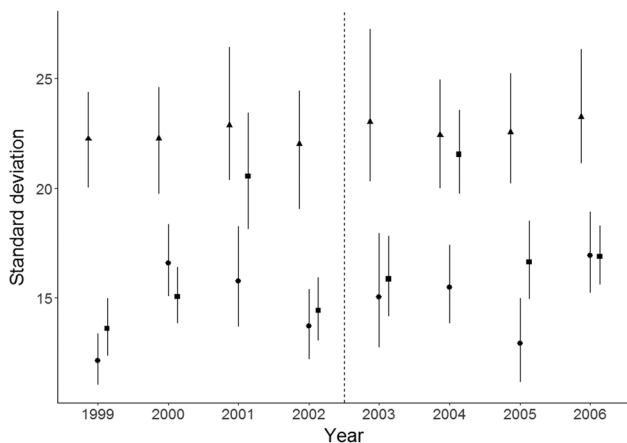

Figure 4. Estimated standard deviation and 95% credible intervals of date of conception for fawns (triangles), subadult (circles), and adult (squares) female white-tailed deer before (1999–2002) and after (2003–2006) antler point restriction regulations were implemented, Pennsylvania, USA. The dashed vertical dashed line indicates when regulation changes could have affected a change in conception date.

Table 3. Model selection statistics to investigate if reproductive characteristics changed when sex-age characteristics of the population changed under restrictive harvest regulations for males and increased harvest of antlerless deer beginning in 2002, Pennsylvania, USA, 1999–2006. Age classes were the age of the female when breeding occurred (fawn = 6 months old, subadult = 1.5 yr old, adult = ≥2.5 yr old). The models fitted subadult and adult productivity (embryos per female), fawn pregnancy rate (proportion pregnant), and embryo sex ratios for subadult and adult females over time.

Model	ΔAIC[c]	AIC[c] weight	Number of parameters	Log-likelihood
Subadult female productivity				
Intercept-only	1.2	0.25	2	−1,642.8
Before vs. after[a]	0.0	0.45	3	−1,641.3
Transition[b]	0.8	0.30	4	−1,640.6
Adult female productivity				
Intercept-only	0.9	0.27	2	−2,674.0
Before vs. after[a]	0.0	0.43	3	−2,672.6
Transition[b]	0.7	0.30	4	−2,671.9
Fawn female pregnancy rate				
Intercept-only	4.9	0.08	2	−1,194.8
Before vs. after[a]	6.3	0.04	3	−1,194.5
Transition[b]	0.0	0.89	4	−1,190.4
Embryo sex ratio of subadult females				
Intercept-only	0.0	0.65	2	−409.2
Before vs. after[a]	1.9	0.25	3	−409.2
Transition[b]	3.8	0.10	4	−409.2
Embryo sex ratio of adult females				
Intercept-only	0.0	0.65	2	−3,395.8
Before vs. after[a]	1.9	0.25	3	−3,395.8
Transition[b]	3.9	0.09	4	−3,395.7

[a] Response variable differed before (1999–2002) and after (2003–2006) antler point restriction regulations were implemented.

[b] Response variable differed among a) before harvest regulations changed (1999–2002), b) the year harvest regulations changed (2003), and c) following years (2004–2006).
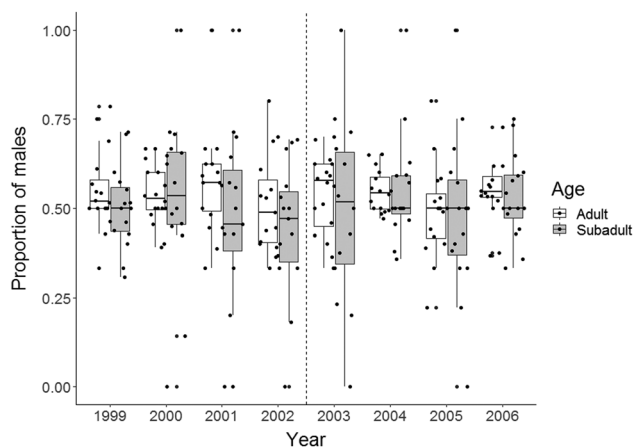
[c] Akaike's Information Criterion.

Figure 5. Proportion of male offspring by age of mother and year for 19 wildlife management units (WMU), Pennsylvania, USA 2002–2009. Each dot represents a WMU, the box represents the median and 25th and 75th quartiles, and whiskers are ±1.5 × inter-quartile range. The dashed vertical line indicates the year after antler point restriction regulations were implemented and potentially could have affected offspring sex ratios.

Sæther et al. (2004) reported that a younger male age structure in moose led to reductions in number of male calves born. Holand et al. (2006) reported that female reindeer impregnated during the second estrus were less likely to produce males and Røed et al. (2007) reported female reindeer that bred with larger males were more likely to produce male offspring. According to the Trivers-Willard model (Trivers and Willard 1973), mothers in better condition are more likely to produce males. Consequently, both improved body condition and more older males could cause the offspring sex ratio to shift towards males.

However, we found no changes in offspring sex ratio for either subadult or adult females during our study. The variation in male:female sex ratio of offspring varied less over time (0.97–1.17) than among DMUs (0.86–1.41), suggesting changes in male age structure had no effect on sex ratio.

White et al. (2001) noted that studies that manipulated adult sex ratios have done so by reducing the density of reproducing females, which confounds the effect of sex ratio and density. Similarly, a limitation of our study was that deer population densities were above management goals so the implementation of APRs to increase the number and proportion of older-aged males in the population required overall deer densities to be reduced (Wallingford et al. 2017). Consequently, we reduced deer densities by 23% and so the potential effects of more older males in the population were confounded by potential improvement in body condition with reduced deer densities. However, we have no evidence that body condition improved based on the lack of change in the percentage of fawns that became pregnant or the lack of increase in productivity in 1.5- and ≥2.5-year-old females.

The Trivers-Willard hypothesis is predicated on the assumption that females in above-average condition should invest more in offspring of the sex with greater variability in fitness. Although studies of polygynous ungulates have generally supported this hypothesis (Kojola 1997), studies of deer in the genus *Odocoileus* have spawned alternative hypotheses to explain variation in sex ratios in this genus (Clark 1978, Williams 1979). Caley and Nudds (1987) suggested that the Trivers-Willard hypothesis provided a weaker explanation of sex-ratio variation in white-tailed deer

and reindeer because these species of deer are less polygynous than red deer (*Cervus elaphus*) and bison (*Bison bison*). Caley and Nudds (1987) noted that for white-tailed deer, compared to red deer or bison, there is less sexual dimorphism, male-biased instead of female-biased breeding groups, and less intensive mate competition. Therefore, the difference between the sexes in terms of variation in fitness may be less in white-tailed deer, which could explain why the change in the adult sex-age structure in Pennsylvania was insufficient to change the sex ratio of offspring.

MANAGEMENT IMPLICATIONS

Harvest regulations, like those implemented in Pennsylvania, that reduce population density, create an older male age structure, and shift the sex ratio towards 1:1 are unlikely to be sufficient to affect the timing and synchrony of breeding, female productivity, and sex ratio of offspring in white-tailed deer. Furthermore, it may be more difficult to influence breeding behavior in temperate environments where climatic conditions may limit variation in timing of breeding. As a result, efforts to identify a desired sex ratio or manipulate sex ratios to achieve management goals on a statewide scale will be challenging.

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