

Maternal life history of white-tailed deer: factors affecting fetal sex allocation, conception timing, and senescence

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ABSTRACT

Questions: How does maternal condition and regional variation in resource abundance affect fetal sex ratio allocation, timing of litter conception, and decreased fecundity due to senescence?

Data studied: We used female white-tailed deer (*Odocoileus virginianus*) maternal age and mass and reproductive tract data (number and sex of fetuses) collected from 1995 to 2011 throughout Alabama.

Methods: *Fetal sex ratio allocation:* We aged collected fetuses to determine conception date and examined the effects of maternal age and mass, litter size, and conception timing (relative to site-specific average conception timing). *Timing of litter conception:* We examined effects of maternal characteristics. *Fecundity:* We examined effects of maternal age and mass. In all models, we assessed the effect of regional variation in resource abundance.

Conclusions: *Fetal sex ratio allocation:* The only significant predictor was conception timing, and sons were more likely as conception date was closer to the peak of breeding. We did not find support for Trivers-Willard or the local resource competition hypothesis. *Timing of litter conception:* Maternal age, mass, and their interaction (maternal age \times mass) explained conception timing, with smaller females conceiving further from the mean conception date among younger females and larger females conceiving further from the mean conception date among older females (likely related to reproductive output in the prior breeding season). *Fecundity:* Not previously demonstrated, we found support for age-related reproductive senescence in female white-tailed deer.

Keywords: conception timing, fetal sex allocation, mammal reproduction, maternal investment in reproduction, *Odocoileus virginianus*, senescence, white-tailed deer.

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INTRODUCTION

Maternal life history can be viewed as a series of complex choices involving trade-offs among known costs, unknown risks, and guaranteed benefits, with the goal being to maximize fitness. Based on one's attributes and environmental conditions, different strategies may be needed to achieve this goal. Theoretically, each breeding episode constitutes another choice, and the body determines if it is physically capable of producing and, in some species, supporting offspring. Trade-offs may be intra-individual or inter-generational; trade-offs may affect not only the maternal individual but also the offspring produced (Stearns, 1989). Females may achieve greater fitness by successfully producing more males than females, as dominant males usually provide the greatest fitness return to mothers, but only if those males are likely to be successful breeders (Trivers and Willard, 1973; Clutton-Brock *et al.*, 1981). However, there is a cost to producing males, as males often require more resources to produce (Clutton-Brock *et al.*, 1981). Therefore, condition is thought to affect not only whether offspring are produced, but how many and of which sex. Condition may also affect when offspring are produced, as individuals in better condition often breed earlier than those in poor condition (Clutton-Brock *et al.*, 1981). Each female should follow the strategy that best suits her current condition and the resources available at each breeding opportunity to maximize her fitness. Fetal sex allocation, optimal timing of litter conception, and declines in fecundity associated with senescence are important aspects of maternal life-history strategy and have evolutionarily significant effects on an animal's fitness.

The number of males and females in a litter of offspring should be a function of attributes of the mother and/or environmental influences. For example, Trivers and Willard (1973) proposed that females in good condition should have male-biased litters because investment in more expensive males would result in a greater increase of her indirect fitness through future reproductive success of a dominant son. On the other hand, females in poor condition should produce more daughters because their reproductive success is less dependent on maternal condition than a son that would have to compete with physically advantaged males for breeding opportunities. Data from numerous Cervid species have shown support for the Trivers-Willard hypothesis [red deer, *Cervus elaphus* (Clutton-Brock *et al.*, 1984); elk, *Cervus canadensis* (Kohlmann, 1999); mule deer, *Odocoileus hemionus* (Kucera, 1991); white-tailed deer, *Odocoileus virginianus* (Burke and Birch, 1995); reindeer, *Rangifer tarandus* (Kojola and Eloranta, 1989)]. However, patterns of fetal sex ratio allocation are by no means fixed. A different hypothesis – local resource competition (Clark, 1978) – posits that the gender composition of litters is more strongly influenced by abundance of local resources, with mothers in good condition investing more heavily in daughters and females in poor condition giving birth to more sons (Caley and Nudds, 1987). This prediction differs from that of the Trivers-Willard hypothesis, but the local resource competition hypothesis reasons that because males are the dispersing sex, a mother residing in areas of low resource abundance gains more by producing the gender – males in many species [e.g. white-tailed deer (Rosenberry *et al.*, 1999)] – that is more likely to disperse from its natal range (Clark, 1978; Hewison and Gaillard, 1996). Put another way, mothers (based upon their own traits and characteristics of their environment) should invest disproportionately more in the gender of offspring with the greatest potential variance in reproductive success. This rule is applicable regardless of which hypothesis is believed to be operating.

To complicate our understanding of the effects of maternal condition and local resource abundance on fetal sex ratio allocation, timing of conception within the breeding season is

also correlated with maternal condition and local resource abundance, but is itself a life-history strategy. Depending upon when conception occurs within a breeding season, timing of parturition may greatly influence either resources available to neonates through direct forage intake, or indirectly through maternal condition and lactation quality (Rutberg, 1987) or risk of predation (Estes, 1976). Consequently, older females in better condition usually conceive in the early and peak stages of the breeding season and are more likely to invest in sons, who may have a physiologically competitive advantage together with a reduced chance of juvenile mortality due to predator swamping. Peak-bearing mothers within more synchronous parturition/conception populations maximize the benefit of predator swamping (Estes, 1976), although there are likely beneficial effects on survival for early births as well (Testa, 2002). Conversely, young adult and juvenile mothers produce the bulk of late-born litters, balancing reproductive investment with maternal somatic growth and maintenance costs (Adams and Dale, 1998; Kohlmann, 1999; Holand *et al.*, 2006; Ditchkoff *et al.*, 2009). Litters with later conception dates are more likely to contain daughters in order to maximize the younger mother's indirect fitness (daughters are more likely to reproduce successfully than sons born later and without the physiological advantages of being born during the optimal period) and direct fitness (daughters require less maternal investment) (Ditchkoff *et al.*, 2009). Thus, it is not known if fetal sex ratio allocation is directly due to mothers' condition and local resource abundance, or primarily due to timing of conception.

If population survival rates allow females to progress through prime-aged adulthood and enter senescence, the dynamics of fetal sex ratio allocation and reproductive investment change. Simply stated, senescence is a decline in reproductive, vital or survival rates with increasing age of an organism (Gaillard *et al.*, 1994; Berube *et al.*, 1999; Ericsson *et al.*, 2001). Fuller *et al.* (1989) reported that old-aged white-tailed deer females had similar mass to sub-adult females, indicating a post-prime decrease in body mass likely resulting in reduced litter size but not necessarily a bias towards female or male offspring (Weladji *et al.*, 2002). Limited data exist regarding fetal sex ratio in relation to senescent reproduction by females. Reproductive senescence can take other forms, including decreased ova production leading to decreased litter size, decreased litter size due to increased resorption rates, and decreased litter survival due to reduced parental investment (Hewison and Gaillard, 2001). While distinguishing between the two causes of decreased litter size may be difficult, especially in studies of wild populations, a reduction in litter size due to either cause would demonstrate reproductive senescence within the species.

Using a large sample of white-tailed deer, the main objective of this study was to examine how fetal sex ratio varies as a function of age and condition of mother, litter size, timing of conception, and regional variation (putatively due to variation in resource abundance). To test the Trivers-Willard and the local resource competition hypotheses, we predicted that maternal condition would be the variable affecting fetal sex ratio most significantly. We hypothesized that due to the complex nature of maternal life history, fetal sex ratio may also be affected by other variables such as age, litter size, timing of conception, and regional variation. Also, we explored the relationship between date of conception and maternal mass (condition) and age, and examined if litter size varied as a function of maternal age, condition, and timing of conception. We hypothesized that older does would conceive before younger individuals and heavier individuals would conceive before lighter ones. We also hypothesized that litter size would primarily be a function of maternal age and condition, with age having a curvilinear effect (i.e. senescence): both young and old individuals would produce smaller litters than individuals of average age. We believe our research to be

valuable because we thoroughly evaluate the relationship between aspects of maternal life history and the possible variables affecting them using a long-term, state-wide dataset collected on deer reproduction in Alabama. These data provide a unique opportunity for testing the above hypotheses, because data were collected randomly (not hunter harvest) from wild populations over a large temporal and spatial scale. The large temporal and spatial scale helped mitigate issues of variation in local resource abundance, while the large dataset allowed us to discern which physical variables were most important to maternal life history.

MATERIALS AND METHODS

We obtained our data on reproductive tracts of female white-tailed deer ($N = 1355$) from the Alabama Division of Wildlife and Freshwater Fisheries. During the spring/summer seasons of 1995–2011, females were collected by sharpshooting as part of the agency's annual white-tailed reproductive surveys. Collections took place from January to July on numerous sites across the state of Alabama (southeastern United States) ranging from public wildlife management areas to large-acreage private landholdings. Annual samples ranged from 9 to 212 (mean = 79.7), and surveys occurred for 2.25 years on average per site (range 1–12 years). White-tailed deer fetuses were backdated to conception date according to the protocol outlined in Hamilton *et al.* (1985). If more than one fetus was present, the average fetal age was used to calculate conception date. Other data collected included site, county (38 represented), Alabama deer management district (as established by the Alabama Department of Conservation and Natural Resources), date of collection, age and unviscerated mass of mother, and number and sex of fetuses. District 1 encompassed northwestern Alabama, District 2 covered northeastern Alabama, District 3 included the west-central region, District 4 encompassed the southeastern quadrant of the state, and District 5 included the southwestern coastal plain (Fig. 1). Females were aged by tooth wear and replacement (Severinghaus, 1949); due to small sample size and increased difficulty ageing older deer, females aged as 8.5 or older were combined into one age category. The full dataset was used in analysis of female reproductive output, while a subset of only pregnant individuals was used to examine conception date and fetal sex ratio ($N = 1129$).

Using the program R (R Development Core Team, 2009), we analysed the potential effects of female age and mass, number of total fetuses, and conception timing on fetal sex ratio using generalized linear models with a binomial distribution in y-values. We used two variables to look at conception timing ('early versus late' and 'days to mean') and never included both variables in the same model. We calculated 'early versus late' and 'days to mean' for each doe based on the average conception date for each site per year (site-year). To do this we calculated the mean conception date for each year of collection for a given site. The 'early versus late' variable was the actual difference between the conception date and the mean conception date, while the 'days to mean' variable was the absolute value of this difference. For example, for a site with a mean conception date of 15 January, a fetus conceived on 22 January would receive a value of 7 for both variables, while a fetus conceived on 10 January would have a value of -5 for 'early versus late' and 5 for 'days to mean'. We only analysed site-years that had at least five females collected. In addition, we tested for effects of maternal age, mass, and the interaction between these two variables on 'early versus late' using a linear model and 'days to mean' using a generalized linear model (family = Poisson). We designated district as a categorical random variable in all models to serve as a surrogate

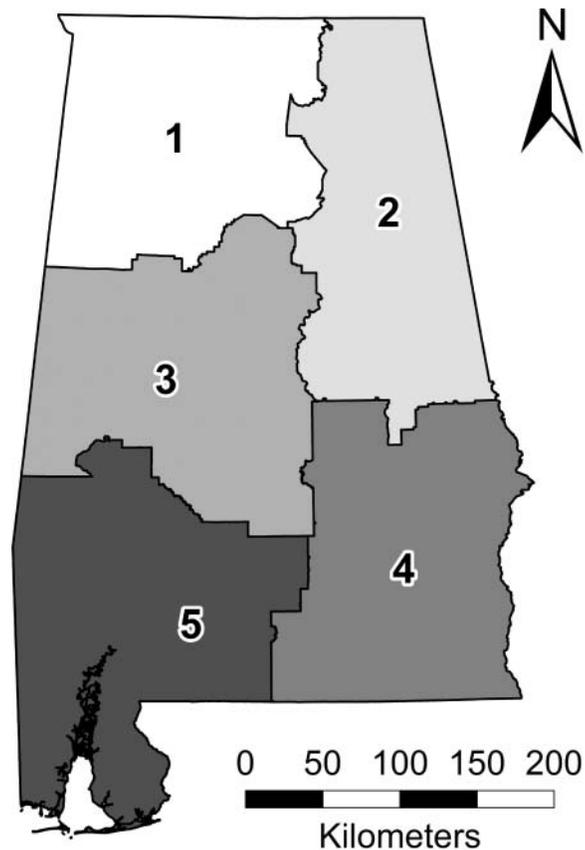


Fig. 1. Map of Alabama Department of Conservation and Natural Resources management regions.

for regional differences in resource abundance. Lastly, we used a generalized linear model (family = Poisson) to analyse the full dataset for female production (number of fetuses produced) as a function of female age, age², and mass.

RESULTS

Fetal sex ratio was fairly uniform across districts with only District 1 being significantly different from Districts 2, 3, and 4 (Fig. 2). Running the global model for the dependent variable fetal sex ratio with the 'early versus late' variable to account for time of conception indicated no significant relationship with independent variables for female age, mass, number of fetuses, and 'early versus late'. The global model with the 'days to mean' variable accounting for conception timing indicated only one significant independent variable: 'days to mean' ($P = 0.047$, $\beta = -0.013$, s.e. = 0.007), meaning that as the number of days to mean conception date increased, daughters were more likely (Fig. 3). Female age, mass, and number of fetuses were not significant. A change in the conception date by one complete oestrous cycle [28 days (Plotka *et al.*, 1977)] resulted in a doe being 1.445 times (confidence interval: 1.200–1.738) as likely to produce a daughter.

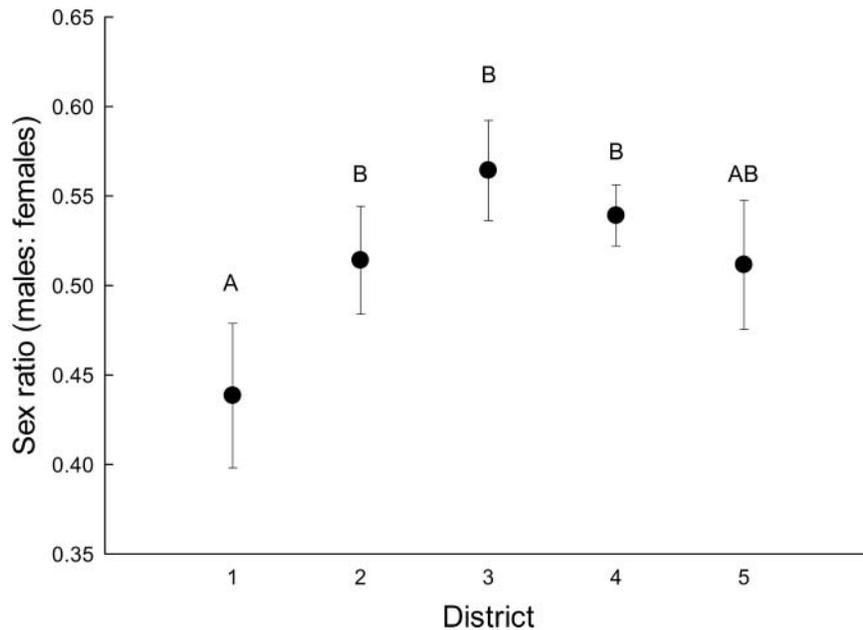


Fig. 2. Fetal sex ratio by deer management district in Alabama averaged across all years (1995–2011). The dataset used in this analysis included only pregnant does ($N = 1129$). Labels A and B indicate which districts are significantly different ($P < 0.05$) from each other.

We found no significant relationship between the conception timing response variable ‘early versus late’ and female age, mass, or the interaction between these variables. However, female age ($P < 0.001$, $\beta = -0.291$, $s.e. = 0.044$), mass ($P < 0.001$, $\beta = -0.031$, $s.e. = 0.003$), and the interaction between these variables ($P < 0.001$, $\beta = 0.007$, $s.e. = 0.001$) were significantly associated with the conception timing response variable ‘days to mean’. Heavier does less than 4.5 years old were more likely to conceive closer to the average conception date than lighter does of the same age, while heavier does older than 4.5 years were more likely to conceive further from the average conception date than lighter does of the same age (Fig. 4).

Pregnancy rates for fawns (6 months old), yearlings (1.5 years old), and adult (≥ 2.5 years old) females were 30%, 91%, and 96%, respectively. The percentage of barren females among older (≥ 7.5 years old) individuals increased slightly to 10.4% ($N = 29$) compared with 3.4% of 2.5–6.5 year old females ($N = 1116$). All litters from pregnant fawns contained one embryo. Pregnant yearling and adult females produced 1.3 and 1.8 embryos per litter, respectively. Figure 5 illustrates the percentage for each litter size by female age and gives the sample size for each doe age. Litters of triplets and quadruplets were produced by 4.6% and 0.2% of pregnant adult female white-tailed deer, respectively, but we did not document triplets or quadruplets in individuals over 6.5 years of age. We found female production was significantly correlated with all considered independent variables – female age ($P < 0.001$, $\beta = 0.249$, $s.e. = 0.066$), age² ($P < 0.010$, $\beta = -0.026$, $s.e. = 0.008$), and mass ($P < 0.001$, $\beta = 0.021$, $s.e. = 0.003$; Fig. 6) – such that fawn production peaked between ages 4 and 5 and declined thereafter, with more fetuses produced by heavier females than lighter females of the same age.

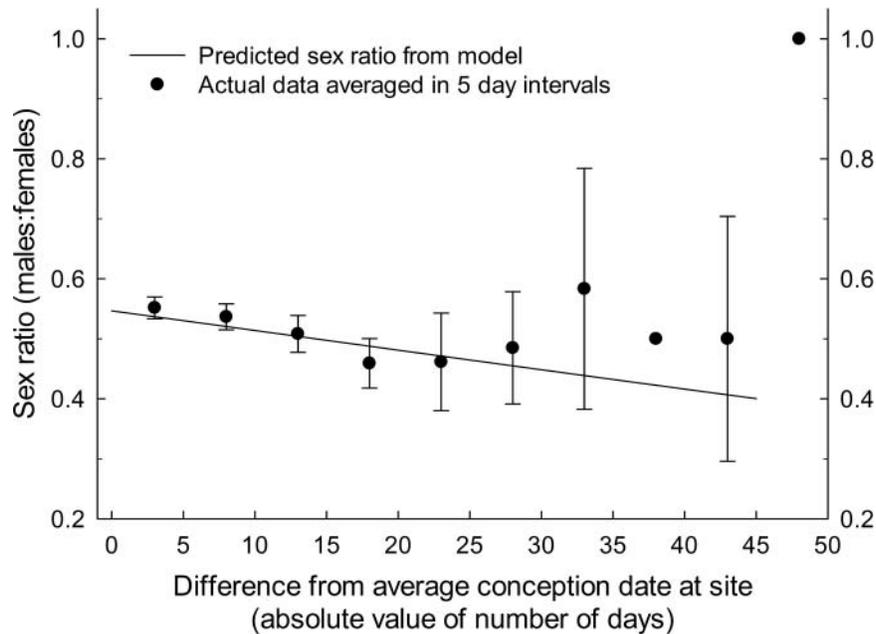


Fig. 3. Relationship between days from average conception (by-site) and fetal sex ratio of white-tailed deer reproductive tracts ($N = 1129$) collected in Alabama, 1995–2011. Within one oestrous cycle, fawns conceived closer to the average conception data were more likely to be male. Small sample size ($N = 6, 1, 4,$ and $1,$ respectively) is likely to have impacted observed fetal sex ratio patterns for >25 days difference.

DISCUSSION

Fetal sex ratio

In global models examining the effect of doe age, doe mass, number of fetuses produced, and conception timing ('early versus late' and 'days to mean', as described in Methods) on fetal sex ratio, the only significant variable was 'days to mean'. The results indicate that the condition of the doe was not a factor in determining fetal sex ratio in this study, and that conception timing was a more important factor than maternal condition. Specifically, the difference between the time of conception and the average conception for a site-year was a better predictor than early versus late season. The lack of a significant relationship between doe mass and fetal sex ratio differs with studies that support the Trivers-Willard hypothesis (Kucera, 1991; Burke and Birch, 1995; Kohlmann, 1999; Sheldon and West, 2004) and the local resource competition hypothesis (Verme, 1969; Clark, 1978; Skogland, 1986; Caley and Nudds, 1987; Hiraiwa-Hasegawa, 1993). Although both hypotheses make predictions about doe condition, rather than mass, we believe that by accounting for age and district of collection (surrogate for resource abundance) in the model, mass becomes an adequate measure of doe condition. Doe age as a single variable has also been shown to have a significant effect on fetal sex ratio (Nixon, 1971; Ozoga and Verme, 1982; Verme, 1983; Richter and Labisky, 1985; Sade, 2004); however, we were unable to detect any effect of age on fetal sex ratio, a result in line with other studies (Monard *et al.*, 1997; Kohlmann, 1999; Weladji *et al.*, 2002; Saalfeld *et al.*, 2007).

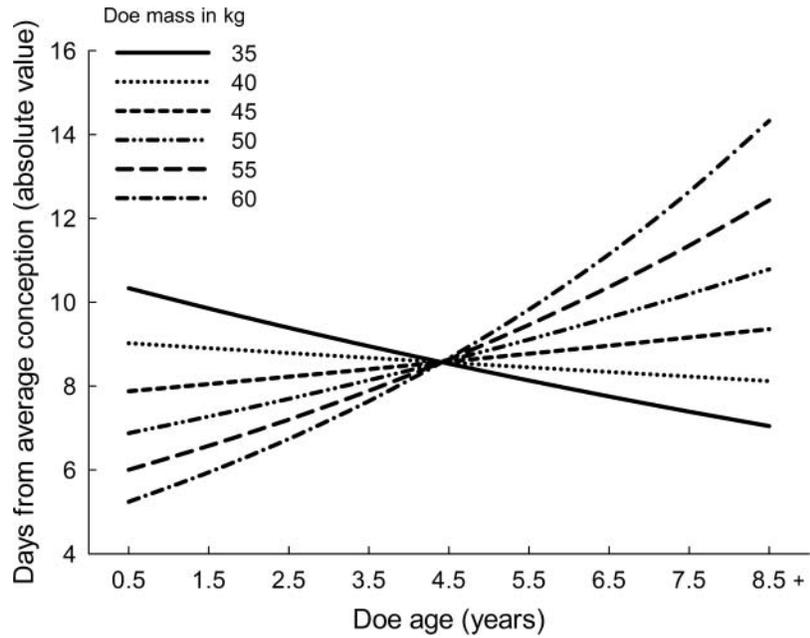


Fig. 4. The global model for the effects of doe age, doe mass, and the interaction between doe age and doe mass on days from average conception for all pregnant does ($N = 1129$) collected in Alabama, 1995–2011.

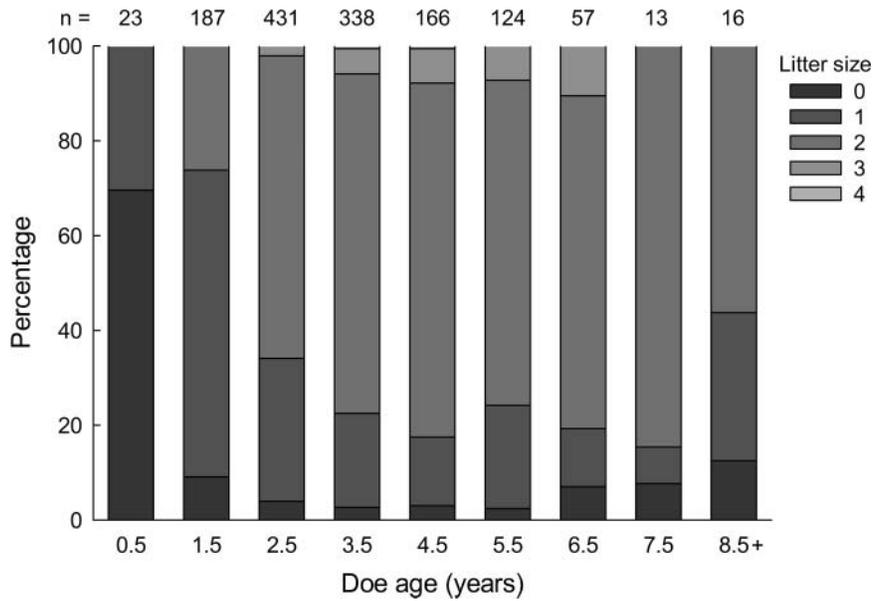


Fig. 5. The percentage of each litter size by doe age for all does ($N = 1355$) collected in Alabama, 1995–2011.

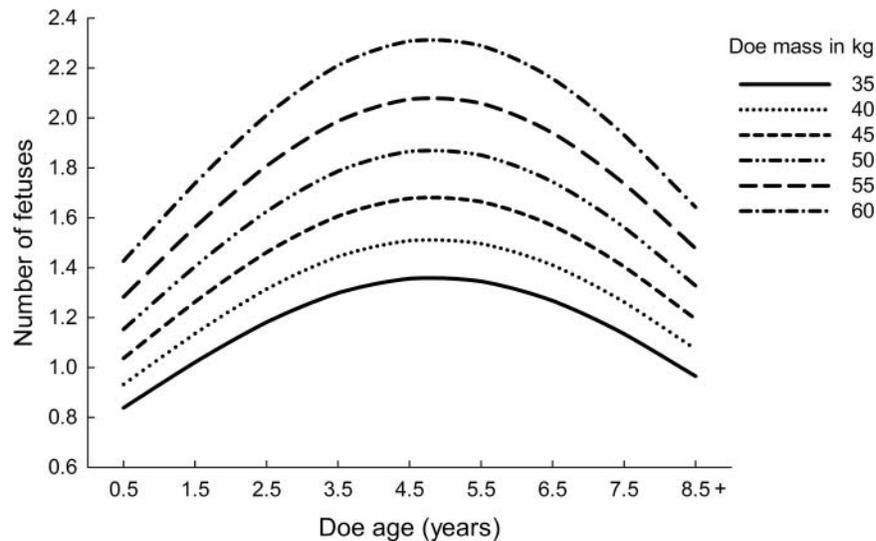


Fig. 6. Effects of age, mass, and age² on the number of fetuses produced by all does ($N = 1355$) collected in Alabama, 1995–2011.

Changes in sex ratio based on timing of conception have been shown in many studies; however, how this timing was measured has varied. Verme and Ozoga (1981) found that more females were conceived within the first 36 hours of oestrus compared with later bred white-tailed does. In contrast, many studies of ungulates have found that females conceiving early in the reproductive season are more likely to produce males or expensive litters than litters conceived later in the season (Kohlmann, 1999; Saether *et al.*, 2004; Hemmer, 2006; Holand *et al.*, 2006; Ditchkoff *et al.*, 2009; Veeroja *et al.*, 2010). We chose to use two variables to look at conception time in different ways – the actual difference in conception timing, ‘early versus late’, and the spread of the conception timing, ‘days to mean’. Both variables use the difference of the site-year average conception date and the individual’s conception date. These variables differ from those in previous studies because they consider changes in sex ratio by season on a much smaller scale than previous population studies, which were state or region wide, often spanning many years. Using variables that account for the mean date of conception is especially important in Alabama where populations are descendants of numerous reintroduction efforts of the early to mid 1900s. These original deer were derived from various and diverse populations resulting in equally variable breeding seasons throughout the fall and winter across Alabama (Lueth, 1967). Population-wide studies have shown that more males tend to be conceived earlier in the breeding season (Kohlmann, 1999; Hemmer, 2006; Ditchkoff *et al.*, 2009; Veeroja *et al.*, 2010); however, our analyses suggest males are conceived closer to the average conception date for a site-year. Consequently, males are likely to be born during the peak of fawning, which may be an advantageous strategy by helping to prevent predation of male fawns due to swamping. Swamping to help prevent predation of fawns is more likely to be advantageous at the local population level, rather than at the regional population level, especially when regional population level conception dates range widely. Swamping has been shown to successfully decrease chances of mortality due to predation,

as young born during non-peak times are more likely to die due to predation (Estes, 1976; Guinness *et al.*, 1978; Gregg *et al.*, 2001).

Due to a lack of available data, we were unable to test for the effects of paternal or maternal status, or differential allocation on fetal sex ratio. Roed *et al.* (2007) supported the differential allocation hypothesis (mothers mating with attractive males may increase fitness by producing more sons, because male offspring may inherit traits conducive to siring success) by showing that female reindeer mating with attractive males produced more sons, and mating was delayed when only young males were present. If white-tailed deer behave similarly to reindeer, a plausible explanation for increased male sex ratio at the peak of conception may be due to females preferentially mating with attractive males and producing more sons compared with when mating with younger males; this would support the differential allocation hypothesis. An alternative hypothesis would be that males during peak rut (which is likely to coincide with peak conception) have high testosterone levels, and testosterone has been known to affect sex ratio (James, 1996).

Date of conception

Owing to the significant interaction term (female age \times mass), our results indicate that for younger white-tailed deer, smaller females conceive further from the average conception date than heavier females, and older heavier females conceive further from the average conception date than maternal females of similar age but smaller size. Because ‘early versus late’ was not significant (but ‘days to mean’ was), there was no discernible temporal bias for time of conception being before or after the mean conception date for older or younger females of different mass classes. Our results and interpretation failed to corroborate the findings of previous studies – adult females breed first, followed by yearlings, and finally fawns (Roseberry and Klimstra, 1970; Johns *et al.*, 1977; Verme, 1989), but indicated that age as well as mass played a significant role in determining timing of conception. Cothran *et al.* (1987) failed to detect a difference in conception date based on maternal age; instead, maternal condition (fat levels) was positively related with early breeding. Although we did not collect data on the previous year’s reproductive output by females [e.g. counting corpora lutea (Cheatum, 1949; Mansell, 1971)], other studies have shown that females that did not gestate during the previous year enter the following season in top condition and conceive earlier than other females (Verme, 1962; Mansell, 1974). Langvatn *et al.* (1994) provide additional evidence that female condition is important in determining conception date for red deer. They found that under high population densities, average body condition declined, and ovulation was delayed even in prime-aged females.

In our study region, there still seems to be a competitive advantage associated with breeding near the peak of conception even with temperate seasonal extremes (Bunnell, 1980). One might expect this phenomenon to be most pronounced in regions of harsh climates and shortened growing seasons, though we do not know of any studies that have examined varying degrees of conception synchrony within ungulate populations. As mentioned earlier, conceiving during the peak of breeding not only has important consequences regarding maternal condition and availability of high-quality forage during parturition, lactation, and weaning, but breeding season synchrony also influences the effectiveness of predator swamping (Estes, 1976; Bunnell, 1980).

Senescence

Our model for female production showed evidence of senescence in white-tailed deer. The bell-shaped relationship (Fig. 6) between number of embryos and age indicated that reproductive output peaked at 4.5–5.5 years of age and declined as individuals aged. Previous studies failed to show senescence among female white-tailed deer, but acquiring adequate sample sizes of older individuals was problematic in some studies (Roseberry and Klimstra, 1970; Nelson and Mech, 1990; Nussey *et al.*, 2008). DelGiudice *et al.* (2007) found no decline in fertility of older females in Minnesota, and older age classes maintained near 100% pregnancy rates. In other species of the Order Artiodactyla, reproductive senescence has been demonstrated in Columbian black-tailed deer [*Odocoileus hemionus columbianus* (Thomas, 1983)], roe deer [*Capreolus capreolus* (Hewison and Gaillard, 2001)], reindeer (Weladji *et al.*, 2002, 2010), bighorn sheep [*Ovis canadensis* (Berube *et al.*, 1999)], moose [*Alces alces* (Ericsson *et al.*, 2001)], and red deer (Carranza *et al.*, 2004; Langvatn *et al.*, 2004; Nussey *et al.*, 2006). The optimal way to examine senescence is to follow individuals throughout their lifetime employing a longitudinal approach (Nussey *et al.*, 2008). In free-ranging white-tailed deer, no research using this study design has been published. Our research, like most other studies, follows a transversal study design (based on a cross-section of a life table) in which each female was only sampled once at the time of death (Gaillard *et al.*, 1994).

CONCLUSION

The only factor directly affecting fetal sex ratio allocation was how closely females conceived relative to the peak of breeding. With no difference in the effect of early versus late conception timing on fetal sex ratio, it is apparent that the window of peak conception is optimal because of pressing factors present both before and after that period. Also, timing of conception was affected by maternal age and mass and suggested that large-bodied, mature females (possibly in better condition because the previous year's litter/offspring was stillborn or depredated) bred on the fringes of the peak conception period, while younger females in prime condition conceived closer to the peak of breeding. Although we did not detect a direct effect of maternal condition (in our analysis, mass as adjusted for by age and resource abundance) on offspring sex ratio, the linking of the fetal sex ratio and date of conception analyses suggests an indirect effect is present. Explicitly stated, conception timing ('days to mean', specifically) was a function of maternal mass, maternal age, and their interaction, while 'days to mean' (i.e. conception timing) was the only variable with a direct effect on fetal sex ratio allocation. A complex relationship, the indirect effect of condition through conception timing is certainly present. Biologically, this indirect effect of condition on fetal sex ratio could be explained, at least in part, by the female's condition controlling when ovulation/conception occurs, so that a male's testosterone levels at copulation would influence her litter's offspring sex ratio composition to be of the greatest benefit to the female based on her condition. This possible explanation assumes that paternal testosterone levels affect sex ratios, as reported by James (1996). The complexities described above raise the possibility that other studies that have dismissed the role of condition in maternal fetal sex ratio allocation may not have been thorough enough to uncover more subtle support for condition-dependency. Finally, and as expected, post-mature female white-tailed deer in poorer condition exhibited a decline in reproductive output. All evidence supports the assertion that white-tailed deer

reproduction, and ultimately fitness, is sensitive to an intricate array of physiological and biological factors.

ACKNOWLEDGEMENTS

We thank the Alabama Department of Conservation and Natural Resources for providing the data for this study. This research was supported by funds from the Three Notch Wildlife Research Foundation and the Auburn University Deer Lab. Finally, we appreciate Dr. Daniel Rubenstein's thought-provoking and beneficial comments on the manuscript.

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