

## Factors Affecting the Number of Fetuses in a White-tailed Deer Herd

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*Abstract:* Data were taken on 1,103 pregnant white-tailed deer (*Odocoileus virginianus*) harvested from the Savannah River Plant in South Carolina from 1965–1985 to describe temporal, age specific, and habitat effects on fetal number. Time periods were thought to represent periods of high and low population density. Age was the most significant factor in altering fetal number both with and without the data from the fawns included. Low fetal numbers per doe in 0.5- and 1.5-year-old deer and a high incidence of twinning in the older deer was responsible for this effect. Mean number of fetuses per doe for the 0.5-year-old deer ( $x = 1.06$ ) was less than for 1.5- ( $x = 1.56$ ), 2.5- ( $x = 1.73$ ), and  $\geq 3.5$ - ( $x = 1.76$ ) year-old age classes. Temporal and age specific effects among time periods on fetal number were significant in the analyses using data from all age classes. These effects were probably not related to density dependent feedback mechanisms, but rather to a sampling bias due to differential representation of deer of different ages or origin in the statistical analyses. Significant differences were observed in fetal numbers between females from the swamp and upland areas both with and without the data for the fawns. Differences between the densities, and/or habitat quality in the 2 areas were responsible for this effect.

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Estimates of reproductive performance are essential for understanding the dynamics of a population. Reproductive rates vary with age and nutrition in many mammals. Temporal, age-specific, and habitat-related effects have been shown to influence fetal numbers in white-tailed deer (*Odocoileus virginianus*) (Teer et al.

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1965; Verme 1965, 1969; Ransom 1967; Haugen 1975). Consequently, temporal and regional variability in population age structure or density and/or concurrent variability in the nutritional quality of a habitat will likely result in differences in reproduction over time and space. Frequently reproductive and demographic data for deer from 1 area covering a range of habitats, densities, and age structures over long periods of time are lacking.

Intensive either-sex hunting of deer at the Savannah River Plant (SRP) has resulted in documented changes in population density and age structure that are attributed partially to existing populations in different habitat types on the site (Urbston 1976, Dapson et al. 1979, Ramsey et al. 1979). Previous studies on the SRP have documented variation in age and habitat-specific fetal numbers (Johns et al. 1978) and significant variation in numbers of fawns breeding in 2 habitats in response to fluctuations in population density, age structure, and habitat quality (Urbston 1967, 1976). The effects of genetic variability on reproduction in white-tailed deer on the SRP and differences in the levels of genetic variability between deer in different habitat types also are documented (Johns et al. 1978, Ramsey et al. 1979, Chesser and Smith, In press).

Deer densities, age structures, and habitat quality vary between swamp and upland areas on the SRP (Dapson et al. 1979, Harlow et al. 1979). These data in combination with age-specific fetal data allow an analysis of the factors affecting litter size in white-tailed deer. The objectives of this study were to describe the effects of age, habitat, year, and their interactions on litter size in white-tailed deer on the SRP.

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## Methods

Deer were collected on the SRP from 1965–85. The site (810 km<sup>2</sup>) is located in Aiken, Barnwell, and Allendale counties in west-central South Carolina. The SRP is bordered on the south and southwest by the Savannah River. The SRP deer herd originated primarily from small groups of deer inhabiting the inaccessible bottomland areas at the time of site acquisition (Jenkins and Provost 1964). As deer numbers increased, controlled deer hunts were initiated on the site in 1965 in an effort to lower a high rate of train-deer and car-deer collisions.

The SRP is composed of 50 compartments that can be divided into swamp and upland areas (Urbston 1967). The swamp area of the plant encompasses planted pine (*Pinus* spp.) and bottomland hardwood areas that border a deep water cypress-tupelo-gum (*Taxodium* spp. - *Nyssa aquatica*) swamp. The upland area is characterized by planted pine and mixed pine-hardwood stands.

Data were collected at check stations during fall hunts held on the SRP from 1965–84. From 1965–80 both dog and still hunting methods were used. Thereafter only dog hunting was used (Scribner et al. 1985). Additional collections were made during the winter and/or spring in the periods 1965–70, 1975–77, and 1985. Analyses were conducted on a total of 1,103 visibly pregnant females collected over this period. Females were classified as pregnant if an embryo or fetus was visible upon an inspection of the uterus. Percent pregnancy was not calculated because the timing of the fall hunts did not allow an exact estimate. Age was determined by tooth eruption and wear (Severinghaus 1949). Location, date of kill, body weight, lactation, and number of fetuses were recorded for each animal collected.

Variation in fetal numbers among females was examined according to age class, time period, and habitat. The analyses were performed with and without the data from fawn females. The variables of fetal numbers ( $N$ ), age class ( $A$ ), habitat type ( $H$ ), and year ( $Y$ ) were used in log linear analyses (G-test; Sokal and Rohlf 1981) using the BMDP statistical software package (Dixon et al. 1983). Statistical significance was accepted at  $P < 0.05$ . Fetal number was identified as either 1 or  $\geq 2$  fetuses for each pregnant doe for this analysis. However, mean fetal numbers were calculated using exact fetal number. Females were divided into 4 age classes; 0.5, 1.5, 2.5, or  $\geq 3.5$  years old. Habitat type was defined as swamp or upland habitat because previous studies had noted its importance to fetal numbers and incidence of fawn breeding on the SRP (Johns et al. 1978, Urbston 1976). Four time periods were considered: 1965–70, 1974–77, 1978–81, 1982–84. Data from single years were pooled to alleviate the problem of low sample size in some years. Year periods reflect times of high and low density with periods 1 and 4 representing relatively low densities and periods 2 and 3 relatively high densities (Dapson et al. 1979).

## Results

Age had a significant effect on fetal number with and without the data for fawns added to the analysis. Twinning was higher in the older deer. Fetal numbers were highest in the females  $\geq 3.5$  years old followed by those 2.5, 1.5, and 0.5 years old (Table 1). Age specific variation in fetal number was still significant without the data from the fawn age class due in part to lower reproduction in the 1.5-year age class ( $P < 0.0001$ ; Table 2). Mean fetal numbers calculated as a weighted average of transformed values with ( $x = 1.63$ ) and without ( $x = 1.66$ ) the data from the fawn age class were not significantly different (Table 1).

Age-specific variation in fetal numbers was not consistent over time periods (significant  $N \times A \times Y$  interaction for all age classes; Table 2). This significant interaction was not observed when the data from the fawn age class were removed from

**Table 1.** Summary of mean number of fetuses per pregnant female and number of pregnant females (in parenthesis) for each age class in the swamp and upland areas during 4 time periods. Means are given by year, age class, and area.

Area	Time Period	Age Class (Years)				Means (Years)	
		0.5	1.5	2.5	≥3.5	≥0.5	≥1.5
<b>Swamp:</b>							
	Period 1 1966-70	1.00 (5)	1.45 (14)	1.47 (23)	1.69 (30)	1.52 (72)	1.57 (67)
	Period 2 1974-77	1.00 (4)	1.29 (24)	1.62 (36)	1.66 (34)	1.52 (98)	1.55 (94)
	Period 3 1978-81	2.00 (1)	1.42 (15)	1.74 (9)	1.38 (7)	1.51 (32)	1.50 (31)
	Period 4 1982-84	1.00 (2)	1.56 (33)	1.61 (26)	1.71 (24)	1.60 (85)	1.62 (83)
<b>Average</b>		1.07 (12)	1.44 (86)	1.59 (94)	1.66 (95)	1.54 (287)	1.57 (275)
95% CI <sup>a</sup>		0.93- 1.22	1.38- 1.50	1.48- 1.70	1.55- 1.77	1.51- 1.58	1.50- 1.63
<b>Upland:</b>							
	Period 1 1966-70	1.05 (18)	1.56 (18)	1.62 (6)	2.00 (8)	1.43 (50)	1.68 (32)
	Period 2 1974-77	1.00 (5)	1.62 (66)	1.77 (94)	1.72 (55)	1.69 (220)	1.71 (215)
	Period 3 1978-81	1.36 (5)	1.53 (61)	1.76 (107)	1.68 (36)	1.68 (209)	1.69 (204)
	Period 4 1982-84	1.00 (13)	1.63 (104)	1.71 (134)	1.75 (86)	1.67 (337)	1.69 (324)
<b>Average</b>		1.06 (41)	1.60 (249)	1.75 (341)	1.73 (182)	1.66 (816)	1.70 (775)
95% CI <sup>a</sup>		1.00- 1.13	1.53- 1.67	1.58- 1.93	1.66- 1.81	1.63- 1.70	1.66- 1.73
<b>Combined</b>							
<b>Average<sup>b</sup></b>		1.06 (53)	1.56 (335)	1.73 (435)	1.76 (277)	1.63 (1103)	1.66 (1050)
95% CI <sup>a</sup>		1.00- 1.12	1.50- 1.61	1.64- 1.77	1.72- 1.78	1.60- 1.66	1.63- 1.70

<sup>a</sup>95% Confidence intervals and means as calculated from square root transformed fetal numbers but expressed as untransformed values.

<sup>b</sup>Mean fetal number for age classes ≥1.5 years for both habitat types combined expressed as weighted mean is  $\bar{x} = 1.72$ .

**Table 2.** G-tests of significance and interaction among the variables of Female Age (*A*), Time Period (*Y*), Habitat Type (*H*), and Fetal Number (*N*) in white-tailed deer from the Savannah River Plant in South Carolina. Analyses were performed with and without the data from the 0.5-year female age class.

Hypothesis Tested <sup>a</sup>	All Ages			>1.5 Years		
	G	df	P	G	df	P
<i>N</i> × <i>A</i>	105.1	3	<0.0001	23.8	2	<0.0001
<i>N</i> × <i>Y</i>	12.6	3	0.005	2.6	3	0.461
<i>N</i> × <i>H</i>	12.6	1	0.0005	15.1	1	<0.0001
<i>N</i> × <i>A</i> × <i>Y</i>	18.11	9	0.034	11.6	6	0.071
<i>N</i> × <i>A</i> × <i>H</i>	3.2	3	0.368	1.14	2	0.564
<i>N</i> × <i>Y</i> × <i>H</i>	1.6	3	0.658	1.28	3	0.733
<i>N</i> × <i>A</i> × <i>Y</i> × <i>H</i>	6.34	9	0.698	1.24	6	0.975

<sup>a</sup>*N* = 1 or ≥2 fetuses; *A* = 0.5, 1.5, 2.5, or ≥3.5 years old; *Y* = 4 time periods (Table 1); *H* = swamp or upland areas.

the analysis, although the trend was in the same direction and was nearly significant ( $P = 0.07$ ). Significant variation in the fetal number to age relationship was correlated with variation in the sample size for breeding fawns. Age-specific variation in fetal number was consistent between habitat types (non-significant  $N \times A \times H$  interaction). Fetal number varied significantly among time periods, but not when the analysis was performed without the data from the fawns. Variation in fetal number among time periods was not significant between habitat types (non-significant  $N \times Y \times H$  interaction).

Significantly higher mean fetal numbers were observed in the upland ( $\bar{x} = 1.66$ ) than in the swamp ( $\bar{x} = 1.54$ ) when considered over all ages (Tables 1 and 2). The variation in mean fetal numbers between deer from different habitat types was reflected only in the adults  $\geq 1.5$ . This trend was found in all time periods but was significant for deer from periods 2 and 3 ( $x^2 = 7.23$ ,  $P 0.01$  and  $x^2 = 4.38$ ,  $P < 0.05$ , respectively). Mean fetal numbers for fawns was not different between the swamp and uplands (Table 1). The effect of fawn breeding on the overall fetal number for upland females was not significant ( $\bar{x} = 1.66$  and  $1.70$  calculated with and without data from the fawns, respectively). Due to small adult sample size, a reduction in overall reproduction was observed in period 1 in the upland with the fawn age class included. The lower fetal number in adult females in the swamp is responsible for the habitat effect on fetal number.

## Discussion

Female age accounts for most of the variation in fetal number in white-tailed deer on the SRP (Tables 1 and 2). Fetal numbers in the fawn and 1.5-year age classes are low when compared to those of older animals (Table 1). These data are consistent with the results of other studies on white-tailed deer (Olmstead 1970; Kirkpatrick et al. 1976; Richter 1981), red deer (*Cervus elaphus*) (Clutton-Brock et al. 1982), and mule deer (*Odocoileus hemionus*) (Wallmo 1981) which show lower fetal numbers in the fawn and sub-adult age classes than in the older adults.

As young animals mature, they must partition their metabolic resources between growth and reproduction. As a deer reaches asymptotic weight, the proportion of energy used for growth decreases to zero and that for reproduction is maximized. During the fall, fawn females have reached approximately 50% of asymptotic weight and 1.5-year-olds approximately 85% (Chesser and Smith, In press). Both the 0.5- and 1.5-year-old females have significantly lower levels of body fat during the breeding season than the older females (Johns et al. 1984), thus indicating a potentially limited energy resource or a limited ability to process available resources for maximal growth and reproduction. Calculations for the SRP herd of energy demands on females during gestation and lactation demonstrate that most of the energy required by a female to produce a fawn comes from daily ingestion rather than fat reserves (e.g. Cothran, pers. commun.). The combination of low fat reserves and high energy requirements for growth in the younger deer produces fewer breeding animals and lower fetal numbers in those that do breed. Pregnant fawns are represented in this sample in lower proportions, because of their lower rates of pregnancy (Urbston 1976; Johns et al. 1978). The effects of changing resource availability and/or quality should be more readily detectable in the 0.5- and 1.5-year-old deer than in the older ones (Verme 1967; Harder 1980).

Fetal numbers ( $N \times Y$ ) and the pattern of age-specific effects on fetal numbers  $N \times A \times Y$  varied over the 4 time periods of this study (Table 2). Fetal number was lowest in period 1 when density was low, but the effect is dependent upon inclusion of the fawn data. The proportion of pregnant fawns in the sample is highest in period 1, and the time period effect is probably due to including more fawns with single fetuses in the first as compared to the latter periods. Thus, year and age effects are confounded by a sampling bias reflected in the differential representation of the 4 age classes in these time periods. Differences in density are not likely the cause of the year effect on fetal numbers. A similar argument can be made for the age-specific variation over time periods since the proportional representation of the deer from the swamp and upland areas vary dramatically in the 4 time periods (Table 1). For example, the pattern of age-specific differences would primarily be determined by deer from the upland during period 3 and by those from the swamp during period 1. The very low fetal numbers of 1.5-year-old females in the swamp during period 2 could be interpreted as an effect due to high densities or random sampling variation. In addition, none of the interactions involving both habitat and time period are significant.

There is no evidence for the importance of density dependent feedback occurring differentially over years despite the range in densities observed (Dapson et al. 1979) and evidence for such a feedback in another herd (McCullough 1979). Mean fetal number for females 1.5-years old or older ( $\bar{x} = 1.72$ , expressed as a weighted average) on the SRP is higher than comparable values for deer from Florida (1.28, Harlow 1965), Mississippi (1.61, Jacobson et al. 1980), and Michigan (1.36, Eberhardt 1969), but not for deer from Illinois (1.88, Roseberry and Klimstra 1970). White-tailed deer on the SRP have and are reproducing at a high level that is characteristic of a herd considerably below carrying capacity.

The best evidence for density effects is the difference between mean fetal number for deer in the swamp and upland areas (Table 1;  $N \times H$ , Table 2). Deer from the 2 areas differ in a number of characteristics including genetics (Ramsey et al. 1979), demography (Dapson et al. 1979), morphology (Brisbin and Lenarz 1984), and quality of diet (Harlow et al. 1979). The densities in the 2 areas have differed by more than twofold, with the higher level being in the swamp (Dapson et al. 1979). Estimates of forage quality and density in the 2 areas suggest that deer in the swamp are closer to carrying capacity than those in the uplands (Moore 1967; Dapson et al. 1979). Thus, the lower fetal numbers in the swamp are expected. McCullough (1979) observed an inverse relationship between size of the post-hunt population and fetal number in the George Reserve herd. Although density effects may not be important in explaining annual variation in fetal numbers, they seem important in accounting for the habitat differences.

Reproductive performance in a population may vary as a function of its environment and level of genetic variability. Reproductive characteristics of a herd may reflect different genetic effects and/or habitat quality. Overall levels of genetic variability are higher for females sampled from the swamp than for those from the uplands (Johns et al. 1978; Ramsey et al. 1979). Females that are more heterozygous tend to reach asymptotic body weight later and have 2 fetuses more often than do their more homozygous counterparts (Johns et al. 1978; Chesser and Smith, *In press*). In view of these trends and given equal resources per animal, it would be expected that females in the swamp would have higher mean fetal numbers and a lower incidence of fawn breeding than those in the upland. There is a lower incidence of fawn breeding in the swamp (Urbston 1976), but the mean fetal numbers also are lower (Table 1). Density dependent feedback mechanisms seem more important in accounting for differences in fetal numbers for deer from the 2 areas than do genetic factors. The differences between fetal number might have been even larger, if the genetic characteristics of the deer had been the same in each area.

Age structure was more important in altering fetal number than were habitat effects, but the relative importance of demography, habitat, genetics and their interactions still need to be evaluated for white-tailed deer living under different levels of density.

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