

REPRODUCTIVE PATTERNS, PRODUCTIVITY AND GENETIC VARIABILITY IN ADJACENT WHITE-TAILED DEER POPULATIONS

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Abstract: White-tailed deer (*Odocoileus virginianus*) were collected from swamp and upland areas on the Savannah River Plant in South Carolina; the genetic variability of females was 9.8 and 8.5%, respectively, for the 2 areas. Reproductive rates (92-93 fawns/100 females) were essentially the same in the 2 areas. Deer in both populations, age ≥ 2 yr, bred earlier and showed less variance in conception dates than younger deer, and swamp deer bred earlier than upland deer. In the swamp, deer with 2 fetuses had significantly higher levels of genetic variability than those with 1 fetus, and the trend although not significant was the same in the uplands.

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Four factors which change the number of individuals in a population are reproduction, mortality, emigration and immigration. Usually management of wildlife populations deals with only the first 2 of these and attempts to maximize reproduction while minimizing mortality caused by sources other than harvest techniques. In a practical sense, reproduction as a manageable characteristic is easier to measure than mortality. For white-tailed deer, the number of fawns produced in a population of a given size is an important measure of the status of that population. The percentage of females that have young, average number of fetuses per pregnant does and age structure of the population are important determinants of the rate of productivity. Even though numerous studies have been made on the white-tailed deer, relatively few have resulted in productivity estimates, and geographic variation in this measure might be expected.

Productivity can be influenced by both environmental and genetic factors. Much work has been done on environmental factors, but genetic effects on productivity have seldom been investigated in natural populations. One study dealing with natural mammalian populations indicated that productivity was positively related to the overall level of genetic variability (Smith et al. 1975). Similar studies are needed for wildlife populations. Thus, our objective was to study the reproductive biology of 2 adjacent herds on the Savannah River Plant (SRP) in South Carolina and to test for the importance of the influence of genetic variability on the reproductive performance of white-tailed deer.

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MATERIALS AND METHODS

The SRP in South Carolina was acquired by the Atomic Energy Commission during 1950 and 1951 and was officially closed to the public on December 14, 1952. The 80,971 ha area lies in Aiken, Barnwell and Allendale counties and is bordered on the south and southwest by the Savannah River. The SRP herd presumably originated from a small (25 or less) herd living in the swamp along the Savannah River at the southern extremities of the site (Jenkins and Provost 1964). In the fall of 1965, limited public hunting was initiated to slow the growth of the rapidly expanding deer population.

Deer habitat is now considered excellent over much of the SRP. Prior to government

acquisition the farmland provided little suitable habitat and continual hunting kept deer numbers very low. Deer now occupy all parts of the SRP, which can be divided into 2 major areas, swamp and upland. The swamp is composed of lowland hardwoods with numerous cypress (*Taxodium distichum*) and tupelo gum (*Nyssa aquatica*) trees and is bordered by the uplands which is characterized by pine (*Pinus* sp.) plantations with hardwoods along the stream bottoms and around abandoned homesites.

We collected approximately 260 females ranging in ages from 0.5 to 8.5 years from 15 December through 15 June. Public hunts, conducted by the U.S. Forest Service during 1975 and 1976 were supplemented by winter and spring collections during 1976 and part of 1977 along secondary roads, railroad cuts and powerlines by shooting with a high velocity rifle. Breeding dates were determined for pregnant females by aging fetuses (Armstrong 1950) and backdating to the date of conception. A gestation period of 200 days was used as the upper limit of prenatal age.

Liver and blood samples were taken, processed and analyzed using horizontal starch-gel electrophoresis for 28 biochemical loci (Manlove et al. 1975). Systems examined included esterases 1, 2, 3 and 4, alpha- and beta-hemoglobin, albumin, transferrin, acid phosphatase, phosphoglucose isomerase 1 and 2; phosphoglucomutase 2, indophenol oxidase, glutamate oxalate transaminase 1 and 2, alpha glycerophosphate dehydrogenase 1 and 2, glucose-6-phosphate dehydrogenase, glutamate dehydrogenase, isocitrate dehydrogenase 1 and 2, lactate dehydrogenase 1 and 2, malate dehydrogenase 1 and 2, malic enzyme, 6-phosphogluconate dehydrogenase and sorbitol dehydrogenase.

Statistical analyses were performed using the Statistical Analysis System (Barr et al. 1976).

RESULTS

The length of the breeding season on the Savannah River Plant was found to be extensive during the 3 years sampled (Fig. 1). The fawn breeding period occurred during

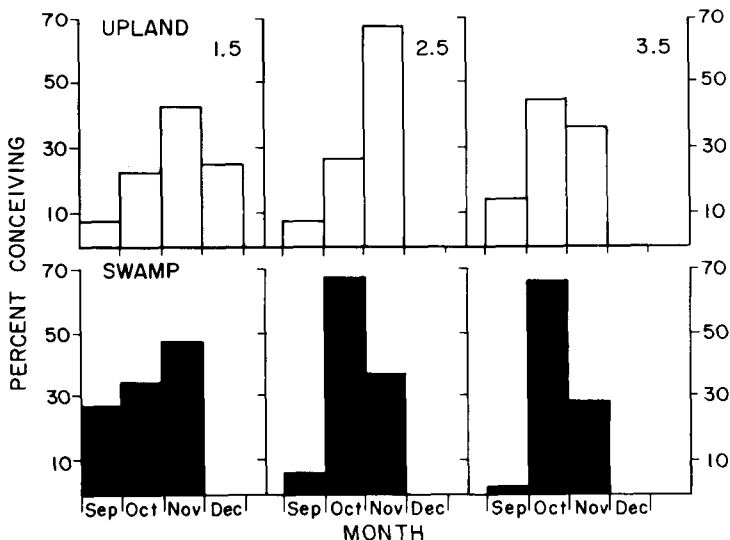


Fig. 1. Percentage of females (N = 128) that became pregnant during the breeding seasons of 1975-77 compared across three age classes and two areas on the Savannah River Plant.

late December through late February while adults bred from mid-September through November. Estimated conception dates for 5 fawns of the previous breeding season were: 12/10, 12/10, 12/27, 12/15, 2/22. The median date of conception was earlier in older deer than younger ones with the following order: 3.5 + < 2.5 < 1.5 < 0.5 yr (< = earlier). This same trend was noted by Paine et al. (1966). Each class in the swamp bred from 1 to 2 weeks before its cohort in the upland (Fig. 1). Where Paine et al. (1966) noted 2 breeding peaks for this herd, we observed only 1 occurring around the

first of November. Fawn breeding did not occur in the swamp during the 1975-76 and 1976-77 breeding seasons, but approximately 5 percent of the fawns in the uplands bred. Data from 16 females during the spring of the 1974-75 season indicated fawn breeding rates of 33 percent in the swamp and 24 percent in the upland.

Data on 102 reproductive tracts indicated a uterine sex ratio of 85 males to 76 females. All fetuses (N = 5) examined from fawns were males. These ratios did not differ from 1:1 but may indicate a slight excess of males as found by Urbston (1972).

The number of fawns produced per 100 does of each age (0.5 to 3.5 +) were calculated for the upland and swamp populations (Table 1). Within each population there

Table 1. Reproductive data for the swamp and upland populations of white-tailed deer on the Savannah River Plant.

Location	Age (Years)	Percent ^a Total Females	Number ^b Females	Percent ^b Pregnant	Embryo Count/ Doe	Fawns Produced/ 100 Does
	0.5	22	20	0	0	0
	1.5	30	25	84	1.52	128
	2.5	30	24	66	1.69	111
	3.5 +	18	15	73	1.54	112
	0.5	32	43	5	1.0	5
	1.5	24	37	73	1.70	124
	2.5	30	47	81	1.76	141
	3.5 +	13	17	88	1.69	149

^aCalculated from 182 and 106 female deer taken from the swamp and upland areas, respectively, during the fall hunt season and spring collections.

^bData given only for females collected after 14 December.

were no significant differences in the proportion of does pregnant in the 1.5 to 3.5 + year old age classes (2 x 3 contingency table analyses; $P > 0.10$). No significant differences were observed in the mean number of embryos per pregnant doe among the 1.5 to 3.5 + year old age classes in either the swamp or upland (one-way analysis of variance; $P > 0.10$). Consequently, the number of fawns produced per 100 does did not differ among 1.5 - 3.5 + year old deer in either the swamp or upland. The reproductive rates of females including fawns were 92.0 and 92.8 fawns per 100 does in the swamp and upland, respectively.

For the combined data, the proportion of pregnant females did not differ significantly between the upland and swamp populations (2 x 2 contingency table analysis; $P > 0.10$). The mean number of embryos per pregnant doe was not significantly different between the upland and swamp populations (one-way analysis of variance; $F = 3.65$; $.05 < P > 0.10$). In contrast to the data in Table 1, the percentage of females pregnant during the late winter and spring (15 January to 1 June) in the various age and location subgroups were as follows: swamp 1.5 - 100%, 2.5 - 100% 3.5 + - 80%; upland 1.5 - 97%, 2.5 - 100%. The sample size for each subgroup exceeded 16 except for the swamp 3.5 + age group that contained only 5 deer. The low sample size in this group may explain the lower value of 80 percent pregnant females. If we assume that essentially 100 percent of the females 1.5 years or older became pregnant then the reproductive rate for the swamp and upland populations were 124.0 and 116.2, respectively. These estimates are probably close to the real values, since the percentage of pregnant females given in Table 1 is probably biased downward due to late breeding females and those that were in the early stages of pregnancy and not visually detectable as pregnant.

The mean level of genetic variability can be expressed as heterozygosity across the 28 loci surveyed. A locus was heterozygous if the maternal and paternal alleles were different on the starch gels. We found the same loci to be variable as those reported by Manlove et al. (1976). The mean heterozygosity of the pregnant females did not differ between locations ($P > .10$) but they did differ within locations between those females having 1 or 2 fetuses (Table 2). In the latter case, the trend for females with

Table 2. Summary of "t" tests for the differences in mean heterozygosities for white-tailed deer females carrying one or two fetuses. The heterozygosities were compared by locality and over the entire Savannah River Plant combined.

Location	Single Fetus		Twin Fetuses		t
	N	Mean Heterozygosity	N	Mean Heterozygosity	
Swamp	22	.0807	44	.1067	2.01 ^a
Upland	29	.0790	89	0.872	.87 ^b
Combined	51	.0800	133	.0937	.13 ^b

^aSignificant at the .05 level.

^bNot significant at the .05 level.

2 fetuses to have higher heterozygosity values than those with one was significant only for the swamp population.

DISCUSSION

Onset of breeding in white-tailed deer has been found to vary with latitude, with a progressively later fawning season in more southerly latitudes (Severinghaus and Cheatum 1956). Differences in breeding peaks, such as we observed, may occur even over a relatively small geographic area as reported for different areas in New York and in North Carolina (Cheatum and Morton 1946; Weber 1966). These differences in breeding peaks have been attributed to variation in photoperiod, rather than to latitude per se (McDowell 1970). This explanation for the differences in the breeding peaks on the SRP is not plausible due to the small size of the area and essentially identical photoperiods. Earlier breeding in the swamp may be attributed to differences in diet and/or relatively low densities resulting from hunting pressure on the swamp population. Urbston (1976) did find a higher percentage of acorns in the rumina of swamp deer compared to upland deer.

Older females tended to breed earlier in the season than younger females (Fig. 1). This was most noticeable in the fawns that conceived as late as 22 February. Later breeding in younger females was also documented on the SRP by Urbston (1976). There was also a trend for increased variance in the conception dates for younger females. The dates of conception are not normally distributed (Fig. 1) and thus, the confidence intervals cannot be given using the standard method without calculating the form of the distribution so that an appropriate transformation of the data could be applied. There is usually a small percentage of males in reproductive condition through late February, and they should be sufficient to impregnate the late breeding females (Payne 1968). It seems that breeding late in the season could put the resulting fawns at a disadvantage by placing the energy demanding period of growth at a time when forage availability is declining (Klein 1965). However, if these late-conceived fawns survive their first winter and reproduce the next year, their mother's contribution to subsequent generations will be greatly increased compared to females that do not breed their first year (Cole 1957).

The number of fetuses per breeding female on the SRP was 1.63, 1.74 and 1.61 for 1.5, 2.5 and 3.5 and older does, respectively. The difference between the number of fetuses per doe in the upland and swamp approached significance (Table 1), but the cause(s) was not apparent and the trend with heterozygosity was opposite to that predicted from the significant effects within the swamp herd. Although the data on fetal number compare favorably with the theoretical maximum of 2 fawns per adult female, the number of fetuses per female was lower than that observed in deer from areas from Texas to Canada (1.85 - 1.98; Ranson 1967; Nixon 1970; Rosenberry and Klimstra 1970; Barron and Howell 1973) but higher than that of coastal plain areas in Georgia (1.1) (Osborne 1976), or Florida (1.2) (Harlow 1965). Harlow (1965) suggested that the lower reproductive rates in Florida and coastal North Carolina deer may be related deficiencies of certain elements in the soil (e.g., cobalt). Perhaps most deer populations occurring on the well drained and highly leached soils of the southeastern coastal plain will be found to have lower reproductive rates than those occurring on other soil types. Emphasis should be placed in future studies on understanding the elemental nutrition of deer from the southeastern coastal plain.

The reproductive rates observed in the upland and swamp were 92.8 and 92.0 fawns produced per 100 females, respectively. In contrast to the information in Table 1, data

obtained from a later part of the reproductive period (15 January thru 1 June) indicate that nearly 100 percent of the female deer 1.5 years of age and older are pregnant. The lower percentage pregnant data in Table 1 are the result of missing the late pregnancies. Assuming the 100 percent figure to be correct for adult females, the estimated reproductive rates are 116.2 and 124.0 fawns produced per 100 females in the upland and swamp areas, respectively. The reproductive rates in the upland and swamp have remained essentially constant since 1966-1967 (108.0 and 103.7 fetuses per 100 does; calculated from data in Urbston and Rabon 1972; Urbston, personal communication), although reproduction among fawns varied considerably from year to year (Urbston 1967, 1976). The reproductive rate stayed essentially the same in spite of the differences in reproductive activity of the fawns because of compensating shifts in the age structure away from younger deer. With increased hunting pressure the percentage of fawns decreased from 49 percent ($N = 37/75$) during 1966-67 to 22 percent ($N = 40/182$) during 1976-77 in the swamp. These percentages are probably high due to selective collecting of smaller deer.

The productivity calculations were made from data on age structure, percentage of females pregnant and mean number of embryos. Since almost all of the females 1.5 years and older became pregnant, the only differences that could change the productivity values in the 2 areas were the percentage of fawn females that became pregnant and mean embryo count. The percentage of fawn females pregnant was similar in the 2 areas (0 vs. 5%; Table 1). Although the mean embryo counts were not different by area, the associated heterozygosity values of the pregnant females did differ by embryo count (Table 2). Females from both the swamp and upland areas with 2 embryos had higher heterozygosities than those with 1 embryo. Urbston (1976) found that gonadal development in male fawns was positively related to increased heterozygosity. In the old-field mouse (*Peromyscus polionotus*) both litter size and productivity are positively correlated with heterozygosity (Smith et al. 1975). Thus, reproduction in mammals seems to be related to genetic heterozygosity, and one goal of an effective management program, might be the maintenance of high levels of genetic variability in local populations.

Differences in important population characteristics even between adjacent locations can be due to either genetic or environmental (e.g., habitat) effects. Estimates of the relative effects of genetics, environment and the interaction of genetics and environment should be made in future studies. Sound management practices should be based on a knowledge of all relevant factors affecting the dynamics of wildlife populations.

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