

## PRENATAL SELECTION IN WHITE-TAILED DEER

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*Abstract:* White-tailed deer (*Odocoileus virginianus*) (N=1341) were collected from 7 locations in Georgia and South Carolina. Sorbitol dehydrogenase (*SDH*) activity was analyzed using starch-gel electrophoresis. Four types of prenatal selection, Female Gametic Selection, Random Mating, Male Reproductive Selection and Female Sexual Selection, were analyzed for this locus using genotype frequency data including mothers and offspring. Spatial and temporal heterogeneity were analyzed for the Savannah River Plant (SRP) herd. Pooled genotype frequencies for *SDH* were essentially the same over 3 years but varied between hunt compartments on the SRP and between the sampling areas across the southeast. All populations were mating at random in respect to the individual genotypes. However, evidence was found for the importance of social structure and intra-uterine events in determining the genetic structure of the herds.

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Recent studies, including many on fish and wildlife populations (Redfield 1974; Moon 1975) have used electrophoretic techniques to document the extensive amount of genetic variation in most species (Powell 1975; Smith et al. 1976). These studies cast doubt that natural populations consist of phenotypically invariant individuals. However, the meaning of this extensive variation is as yet unresolved. The majority of this variation could be neutral and of little use to wildlife managers. Neutrality arguments have come primarily from theoretical grounds and are not based upon studies specifically designed to test the selective value of biochemical variants. Such studies on selection in natural populations are difficult. The controversy over the selective value of biochemical variation does not hinder the use of electrophoretic data (e.g., biochemical markers) in wildlife management programs. In the absence of selective differences, the primary value of these markers would be in studying processes such as dispersal and subdivision of a herd into functional populations.

The high levels of genetic variation present in most species are also in direct contrast to concepts of wildlife management that assume a relatively constant genetic quality for individual animals. When seen, genetic variations in quality are frequently assumed to have little effect in natural populations. Variation in individual quality is usually explained by factors relating to habitat quality. From both an applied and theoretical viewpoint, it is important to know whether most genetically controlled variation can be associated with factors affecting the process of survival and reproduction since they determine the numbers and quality of individuals in a population (Lewontin 1974; Smith et al. 1976).

In previous studies of white-tailed deer biochemical variation for a number of proteins has been documented and the assumed inheritance described (Manlove et al. 1976). Spatial differences in allelic frequency have been shown for B-hemoglobin, and arguments were made for local and regional population differentiation (Manlove et al. 1977; Smith et al. 1976). If biochemical traits are to be of primary importance in a management context they must be correlated with changes in fitness or quality of the organism, i.e., they must modify the selective value of different individuals in the population. The 2 ultimate factors modifying individual fitness are survival and reproduction, and the processes affecting these factors are important.

The purpose of this paper is to further document the use of biochemical variation in testing for populational subdivision in terms of both space and time and to test for

reproductive fitness in terms of prenatal selection in the white-tailed deer. Although we are studying numerous proteins in white-tailed deer populations, Sorbitol Dehydrogenase (*SDH*) was chosen to illustrate the methods of analysis for prenatal selection and the types of results that might be obtained. *SDH* is the enzyme which catalyzes the reaction of sorbitol to glucose, the primary substrate for energy metabolism. This enzyme is found in all wildlife species, and there have been no previous suggestions of *SDH* variation influencing the survival and/or breeding in white-tailed deer populations (Manlove et al. 1976). Also *SDH* is highly variable in all populations studied thus far (Manlove et al. 1976), and provides adequate variation to examine the populations for selection. Prenatal selection partially determines which animals will be available for harvest. Other forms of selection (i.e., survivorship) should and could be analyzed for in this and other species.

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## MATERIALS AND METHODS

White-tailed deer were sampled during the fall hunt season of 1975 from 7 locations in Georgia and South Carolina. The 3 sites in Georgia were the Clark Hill Wildlife Management Area in McDuffie County, the Allatoona Wildlife Management Area in Bartow County, and the Lake Burton Wildlife Management Area in Rabun County. The sites in South Carolina included the Waterhorn Hunt Unit within the Francis Marion National Forest in Berkeley County, the White Oak check station of the Carlisle Hunt Unit in Union County, the Broad River Hunt Unit in Chester County, and the SRP in Aiken and Barnwell Counties. The SRP herd was also sampled during spring 1975, spring and fall 1976, and spring 1977. For the purposes of data analysis, the SRP site was divided into 2 areas based on habitat types: the swamp which borders the Savannah River and the uplands (Urbston 1972).

Samples of liver were collected from adult deer, and either liver or whole body samples of fetuses were collected from the pregnant females. The samples were prepared and analyzed using horizontal starch-gel electrophoresis (Manlove et al. 1976). *SDH* phenotypes were analyzed for prenatal selection using the Selection Component Analysis model developed by Christiansen and Frydenberg (1973). This model utilized mother-offspring data to test 5 hypotheses. These hypotheses were tested by Chi-square analyses of the phenotype-frequency data and are listed in Table 1. Temporal and spatial dif-

Table 1. The hypotheses tested using Selection Component Analysis.

Hypothesis*	In Statistical Terms	In Biological Terms
Female Gametic Selection:	Half the offspring from heterozygous females are heterozygous.	Do eggs with different genes have different probabilities of being fertilized and implanted or do fetuses with different genotypes have different probabilities of survival in utero?
Random Mating:	Gene frequencies in transmitted male gametes is independent of the genotype of the mother.	Do the individuals in the population mate randomly in respect to their genotype?
Male Reproductive Selection:	Gene frequencies in transmitted male gametes equals that in adult males.	Do sperm with different genes have different probabilities of fertilizing eggs or do males with different genotypes have different probabilities of mating successfully?
Female Sexual Selection:	Equal genotype frequencies among pregnant and non-pregnant females.	Do females with different genotypes have different probabilities of mating successfully?
Overall Prenatal Selection:	Combination of the above four tests.	Do fetuses of different genotypes have different probabilities of becoming part of the population?

terences in allele frequencies were analyzed for the SRP herd using Analysis of Variance (ANOVA; Sokal and Rohlf 1969).

## RESULTS

A total of 1,341 white-tailed deer including 331 males, 321 non-pregnant females, 314 pregnant females, and 375 fetal offspring was sampled. Of this total, 897 were taken from the SRP site during 3 winter and spring breeding seasons.

*SDH* had 4 codominant alleles designated *a*, *b*, *c*, and *d*, the last of which was not previously designated by Manlove et al. (1976). This *Sdh<sup>d</sup>* allele migrated cathodally. Allele frequencies for the adults from SRP herd are given in Table 2. Frequencies for

Table 2. Sorbitol dehydrogenase (*SDH*) frequency of the common allele (*c*) from various hunt compartments on the Savannah River Plant during the fall hunt seasons\*. The sample sizes for each year are in parentheses.

Area	Compartment	1974 (N = 325)	1975 (N = 268)	1976 (N = 514)
Upland	15	79.0	77.0	77.0
	17	76.0	83.3	74.0
	18	84.5	79.6	86.9
	20	74.0	80.0	74.4
	25	79.5	80.6	82.3
	32	70.6	69.4	83.3
	42	64.0	73.8	78.8
Mean	46	72.4	82.1	75.8
		75.0	78.2	79.1
Swamp	29	61.8	69.0	67.6
	44	78.3	71.4	74.7
Mean	48	76.9	64.3	78.3
		72.3	68.2	73.5

\*The frequencies of the less common alleles were 1974—*Sdh<sup>a</sup>* = 6.1, *Sdh<sup>b</sup>* = 19.6, and *Sdh<sup>d</sup>* < 1; 1975—*Sdh<sup>a</sup>* = 2.9, *Sdh<sup>b</sup>* = 21.6, *Sdh<sup>d</sup>* < 1; and 1976—*Sdh<sup>a</sup>* = 5.3, *Sdh<sup>b</sup>* = 17.1 and *Sdh<sup>d</sup>* < 1.

adult populations from the other localities were as follows: White Oak - *Sdh<sup>b</sup>* = 26.3 and *Sdh<sup>c</sup>* = 73.7; Broad River - *Sdh<sup>b</sup>* = 25.5 and *Sdh<sup>c</sup>* = 74.5; Waterhorn - *Sdh<sup>a</sup>* = 3.1, *Sdh<sup>b</sup>* = 26.6, and *Sdh<sup>c</sup>* = 70.3; Clark Hill - *Sdh<sup>b</sup>* = 38.0 and *Sdh<sup>c</sup>* = 62.0; Lake Burton - *Sdh<sup>b</sup>* = 61.8 and *Sdh<sup>c</sup>* = 38.2 and Allatoona - *Sdh<sup>b</sup>* = 26.1 and *Sdh<sup>c</sup>* = 73.9. The frequencies of the common allele (*Sdh<sup>c</sup>*) were calculated for deer from 11 hunt compartments on the SRP for the 3 breeding seasons (Table 2). These particular compartments were chosen based on a minimum sample size of 40 deer per compartment for any 2 breeding seasons combined. Three of the hunt compartments (29, 44, and 48) are located in the swamp while the remaining 8 are upland compartments. Analysis of variance of the *Sdh<sup>c</sup>* frequencies across the 11 compartments indicated significant spatial subdivision of the deer herd on the SRP ( $F_{10, 20} = 2.56$ ;  $P < .05$ ). There was no significant variation in allele frequencies across breeding seasons ( $F_{2, 20} = 1.22$ ;  $.10 > P > .05$ ).

Analysis of Female Gametic Selection yielded significant results (Table 3) for the Broad River sample and the 1976-77 SRP swamp and upland samples. The 1975-76 SRP upland sample approached significance, and further examination of the early winter samples (December) for the 1975-76 and 1976-77 breeding seasons yielded significant values (1975 -  $X^2_{1} = 5.00$ ;  $P < .05$  and 1976 -  $X^2_{1} = 6.40$ ;  $P < .05$ ) indicating this type of selection may be a common phenomenon in the SRP upland populations. Only spring samples were available from the 1974-75 breeding season so similar analyses could not be conducted for this period. Heterozygous females would be expected to have 50 percent heterozygous offspring regardless of gene frequencies in the local populations, so the spatial heterogeneity observed for *SDH* would not confound the results of this test. In all herds where the  $X^2 > 3$ , the trend was in the direction of a heterozygote deficiency in the fetuses from heterozygous mothers.

The tests of the second hypothesis, Random Mating, yielded no significant differences over all populations and all years (Table 3). This test may have been affected by the spatial subdivision observed in *SDH*. However, the effects would result in greater  $X^2$  values than observed. The lack of significance is noteworthy in that on an *a priori* basis, one of the test results would be expected to be significant by chance alone (i.e., Type I error with  $\alpha$  set to 0.05; Sokal and Rohlf 1969).

Table 3. Chi-square values for the 5 hypotheses tested (Table 1) using Selection Component Analysis for each locality and for each year at the Savannah River Plant. Values in parentheses are degrees of freedom for each test.

Locality	Adult Sample Size	Female Gametic (1)	Random Mating (2)	Male Reproductive (1)	Female Sexual (2)	Overall Prenatal (6)
White Oak	46	0.00	2.22	0.01	3.53	5.75
Broad River	53	7.36 <sup>b</sup>	2.71	0.56	3.06	13.68
Waterhorn	32	0.00	2.00	0.24	6.14 <sup>a</sup>	8.38
Clark Hill	46	0.14	5.33	1.22	0.95	7.65
Lake Burton	38	0.00	2.92	0.02	6.21	9.15
Allatoona	95	3.00	5.69	1.33	3.09	13.10
SRP Uplands						
Spring 1975	40	0.20	0.06	0.65	4.72	5.63
1975-1976	178	3.27	2.91	0.97	5.72	12.86 <sup>a</sup>
1976-1977	207	3.86 <sup>a</sup>	2.76	1.40	3.12	11.13
SRP Swamp						
Spring 1975	33	1.29	5.73	0.08	1.27	8.37
1975-1976	60	1.29	2.55	8.14 <sup>b</sup>	1.03	13.00 <sup>a</sup>
1976-1977	382	4.00 <sup>a</sup>	0.41	3.93 <sup>a</sup>	0.81	9.15

<sup>a</sup>P < .05

<sup>b</sup>P < 0.1

Analysis of Male Reproductive Selection yielded a pattern of low  $X^2$  values for the majority of populations sampled. The notable exception was the SRP swamp population. The spring 1975 sample continued the trend noted for the majority of populations, however, both the 1975-76 and 1976-77 samples exhibited significant  $X^2$  values and a trend toward a deficiency of heterozygous breeding males. Since pooling populations of differing gene frequencies would yield a disproportionate number of homozygous genotypes in the adult males in comparison to the offspring classes, these tests could be confounded by spatial subdivision of the populations within each study area. Genetic subdivision was characteristic of the 1975 and 1976 samples.

The tests of the fourth hypothesis, Female Sexual Selection, showed significant values for 2 populations, Waterhorn and Lake Burton. These tests could also be confounded by spatial subdivision, but no data were available on the exact sampling locations of the individuals from these 2 areas. These tests compared pregnant and non-pregnant (assumed non-breeders) females from each area, and instead of being a test of female sexual selection, may have been testing differences between early and later breeders. Data on the SRP herd indicate that almost all females become pregnant before the close of the breeding season (Johns et al. 1977). In all cases when  $X^2 > 3$ , there were proportionately more homozygotes among the pregnant females than among the non-pregnant ones.

The overall prenatal selection analysis showed that there were 4 populations with significant  $X^2$  values: Broad River, Allatoona, and the 1975-76 SRP swamp and upland. Two of these, Allatoona and the SRP 1975-76 upland sample, had no other significant tests; however, both had several tests which were close to significance and the effects of all tests were cumulative. The 1975-76 SRP upland sample, when considered for the early winter (December) only, was highly significant for both female gametic selection ( $X^2_{1} = 5.00, P < .05$ ) and male reproductive selection ( $X^2_{1} = 7.65, P < .01$ ), which probably

accounts for the significance for this population. Examination of the genotype-frequency data for the Allatoona population showed no alternate allele homozygotes in the offspring sample, and while no one type of selection can be cited, all probably contribute to the significant lack of alternate allele homozygotes. Four populations showed no significant overall prenatal selection while the individual tests for each population did show some significant differences, indicating that in these cases, the intensity of selection was not great or that the slight interaction of the various types of selection decreased the apparent overall effect.

## DISCUSSION

This study further documents spatial subdivision of local herds (i.e., allele frequencies differ significantly between hunt compartments and localities across the Southeast). Within the SRP, Manlove et al. (1977), showed evidence for at least 3 populations based on the common allele frequency of  $\beta$ -hemoglobin. However, the results of the present study using *SDH* are not totally consistent with the subdivisions described for  $\beta$ -hemoglobin. In the latter case, the deer in compartment 46 were strikingly different from those in the other adjacent compartments, but the *SDH* common allele frequencies were comparable across these compartments. For *SDH*, compartment 29 and to a lesser degree, compartment 42, showed a low frequency for the common allele (Table 2). Thus, the SRP herd is probably split into a minimum of 4 genetically different populations. Whether these populations differ in functional characteristics that are of interest in a management context is still an open question.

While the *SDH* allele frequencies on the SRP were relatively constant, they differed among the various populations sampled across the Southeast. Similar results were obtained for  $\beta$ -hemoglobin (Smith et al 1976). Most areas, including the SRP as a whole, showed an *SDH* common allele frequency of 70 to 76 percent. The exceptions were the Clark Hill and the Lake Burton samples. The Clark Hill sample, with a common allele frequency of 62 percent, was not significantly different ( $P > .05$ ) from the other populations. However, the Lake Burton sample, with a common allele frequency of 38 percent is well beyond the range of the mean frequency plus or minus 2 standard deviations. Manlove et al. (1977) attributed spatial differences in allele frequencies to the social structure of deer which results in limited dispersal and maintenance of localized breeding units. However, differential selection in a heterogeneous environment could also cause the observed patterns even in the presence of high dispersal by juvenile males (Levins 1969).

Pre- and post-fertilization processes can affect the data used to test the 4 hypotheses (Table 1). These processes include such things as competition between males for females, competition between sperm of different genotypes to fertilize eggs, differential implantation fates for fertilized eggs, and differential survival of the fetuses in utero. The lack of significance in the test for random mating indicates that individuals breed at random in the population in respect to genotype. However, certain genotypic classes of individuals could contribute more to the breeding effort than others as evidenced by the significant results for male reproductive and female sexual selection (Table 3). The lack of concordance by locality of the significant results across the random mating, male reproductive and female sexual selection hypotheses makes it unlikely that spatial subdivision in allele frequency can account for the occurrence of the significant results for the latter 2 hypotheses. It appears that homozygous females may breed earlier than heterozygous females, and thus account for the general trend observed for female sexual selection (Table 3). Differential survival and/or implantation of the embryos probably accounts for the significant results for female gametic selection, although differential fertilization of eggs by sperm cannot be discounted.

While the behavioral and physiological mechanisms involved are unknown, the results of the Selection Component Analysis indicate that selection is operating and plays a role in the maintenance of allele frequencies on a microgeographical level. Given the patterns of selection observed, a model can be proposed whereby populations in different areas could be subjected to different selective pressures and regimes. These populations could be subjected to different selective pressures and regimes. These populations could be responding to different environments or could be responding to the environment in different ways. Even among populations of closely related ancestry, no common selective regimes are evidenced. Both the White Oak and Broad River populations were founded (stocked) from individuals of the Waterhorn herd. Although gene frequencies are similar between these populations, their selective regimes are quite different. The parental population, Waterhorn, showed significant Female Sexual Selection for *SDH*, while the Broad River sample showed significant Female Gametic Selection and the White Oak sample seemed free of all 4 forms of selection (Table 3). Populations which are founded

by a small number of colonizers are likely to possess different gene frequencies from their ancestral populations (Berry 1967). In such cases, adaptation to the same environmental type or to different environments may use different gene systems and hence different physiological and/or selective mechanisms (Berry 1970). Our data support a model of microgeographical selection in white-tailed deer.

Temporal changes in common allele (*Sdh<sup>c</sup>*) frequency were not observed in the SRP herd over a 3 year period. Hence, there was no evidence that the observed selection caused an overall directional change in the population in terms of *SDH*. Deer herds are organized into complex social structures (Hirth 1977) composed of different components, such as breeding adult males or non-breeding juveniles. Since the particular individuals that make up these components change through time because of population turnover, the genetic quality of these units probably also varies in time. The types and intensities of the interactions within each social group may result in selection for some optimal balance within the populations yielding essentially no change in allele frequencies for *SDH*. Prenatal selection may act as a fine tuning mechanism that determines the potential interactions of social units. The importance of factors extrinsic to the population (e.g., climate) and their potential interaction with intrinsic factors should not be underestimated. The extrinsic factors could cause long term changes in allele frequency, and the 3 years of this study may be insufficient to detect such changes.

The large amount of observed variation in natural populations could be partially explained by individual differences having no effect on quality or fitness (Kimura and Crow 1964). Using this model, selection would not be expected to act frequently within populations as is clearly the case in white-tailed deer. Christiansen et al (1973) also demonstrated zygotic selection in *Zoarcetes* for the esterase-III locus. More studies of this type are needed to test the neutralist hypothesis by considering selection directly. The explanation of the frequent occurrence of selection will probably be found in Levins' (1969) concept of environment grain in terms of both temporal and spatial coordinates.

The intention of this paper was not to make detailed suggestions for the management of the southeastern herds of white-tailed deer. However, the concept of wildlife populations must surely be modified to include genetic factors that can alter the functioning of certain individuals in these populations. Selection can operate over a short time period to significantly alter a population or to keep it from drifting from some optimal level. While we do not know the precise mechanism(s) that cause the observed deviations in the deer populations, *SDH* is just one of many biochemical systems that might be expected to show selection in this and other species. Further documentation of the occurrence of selection for biochemical and other types of variants in natural populations is needed. These populations are composed of individuals that differ from each other in many characteristics that are differentially correlated with fitness and/or quality through time and space. Finally, this new dynamic concept of wildlife populations needs to be incorporated into the management programs for these biological resources.

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