# BIOCHEMICAL VARIATION AND GENETIC HETEROGENEITY IN SOUTH CAROLINA DEER POPULATIONS[1]

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*Abstract*: Protein variation in 218 white-tailed deer (*Odocoileus virginianus*) from the Savannah River Plant in South Carolina was examined by starch gel electrophoresis. Polymorphism occurred for 7 of 21 structural loci coding for 20 protein systems and for a gene duplication of alpha-chain hemoglobin. Segregating alleles were detected for esterase, transferrin, phosphoglucomutase, glutamic oxalacetic transaminase, malate dehydrogenase, and beta-chain hemoglobin. Swamp and upland subpopulations were recognized from 6 years of data from controlled hunts. The swamp herd had higher but declining density, older age structure, 35% lower fertility among female fawns, and 13% greater mortality of male fawns at the time genetic data were collected. Esterase and hemoglobin loci showed significant differences in genotypic proportions between herds, sexes and age classes. Associated demographic and genetic differences suggest applications of electrophoretic data to management practices by identifying subpopulations, assessing migration, and detecting selection.

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Numerous variables relating to geography, habitat, and demography have been used to define separate populations of game species. With the increased availability and use of techniques such as electrophoresis, genetic variation can be used to further define the biological properties of populations (Selander and Johnson 1973). Electrophoretically determined variants of proteins are used to estimate the degree of polymorphism at a variety of gene loci. These techniques allow a direct comparison of genetic structure across populations or taxonomic groups, provided that functionally similar proteins are utilized (Gillespie and Kojima 1968).

Herein, we describe protein polymorphisms in 2 adjacent populations of white-tailed deer, *Odocoileus virginianus*, from South Carolina. Six years of demographic data had shown these 2 herds to differ widely in survivorship and productivity. Associated differences in demography and degree of protein variation have been shown in voles (Gaines and Krebs 1971) and blue grouse (Redfield et al. 1972). A similar demonstration, which contrasts neighboring groups of deer, would suggest the applications of biochemical variation to management situations.

## METHODS

Two populations of deer were distinguishable on the ERDA Savannah River Plant (SRP) in eastern South Carolina (Urbston 1967, 1972). Data which were collected during fall hunts (1965–71) and by additional sampling each spring, revealed 2 populations with different age structures, sex ratios, and reproductive rates. For each year except 1969, samples

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were taken from within 26 km² which border the continuous bottom-land-hardwood swamp along the Savannah River. Since 1966, yearly samples also were taken from an upland area of approximately 260 km². The uplands is a more diverse area of mixed hardwoods, pine plantations and old-fields. Totals of 1,258 deer from the swamp and 3,750 deer from the upland were necropsied for sex, age (estimated from dentition and tooth wear), and reproductive condition. Ages were assigned in 1-year intervals to fawn (0.5), yearling (1.5), and adult classes (2.5+).

Electrophoretic variation in 21 proteins encoded by 22 structural loci was studied in tissue samples from 218 deer collected during the fall of 1971. Extracts from samples of blood, liver, kidney, heart, and muscle were examined with starch gel electrophoresis. Techniques of electrophoresis and histochemical staining were essentially those of Selander et al. (1971) as described for deer by Manlove et al. (1975). Alleles and protein systems were designated numerically relative to the most anodally migrating bands on gels (Smith et al. 1973:3) except for the hemoglobin systems, where the nomenclautre presented by Harris et al. (1973:270) was used. Their *HB-β* alleles II, III, V, and VII (most anodal) would be designated as *80*, *84*, *92*, and *100*, respectively, in our system.

Five gel types (Electrostarch lots 171 and 271; Otto Hiller, Madison, Wisconsin) and 4 main tissue fractions were used and stained as follows: (1) lithium hydroxide (plasma)—esterase (*ES-1*) and transferrin (*TRF*); (liver)—albumin (*ALB*) and esterase (*ES-2*); (2) continuous tris-citrate, pH 8.0 (liver)—glutamate dehydrogenase (*GDH*) stained as lactate dehydrogenase except 0.5 g L-glutamic acid as substrate, glutamic oxalacetic transaminases (*GOT-1* and *GOT-2*), and malate dehydrogenases (*MDH-1* and *MDH-2*); (kidney)—isocitrate dehydrogenases (*IDH-1* and *IDH-2*); (3) tris-maleate (hemolysate)—esterase (*ES-3*) and 6-phosphogluconate dehydrogenase (*6PGD*); (4) discontinuous tris-citrate or Poulik (liver)—alpha-glycerophosphate dehydrogenase (*αGPD*), phosphoglucomutase (*PGM*), sorbitol dehydrogenase (*SDH*) stained as xanthine dehydrogenase except 0.5 g D-sorbitol as substrate, indolephenol oxidase (*IPO*), and phosphoglucose isomerase (*PGI*); (kidney)—lactate dehydrogenases (*LDH-1* and *LDH-2*); (5) tris-HCl (hemolysate)—hemoglobin alpha-chain II and beta-chain (*HB-$^{II}\alpha$* and *HB-β*).

Three additional protein systems showed poor resolution on the gels and could not be scored with confidence for all individuals. A cathodally migrating alcohol dehydrogenase with buffer system (4) is apparently polymorphic for 2 alleles. Another phosphoglucomutase occurs anodal to *PGM-2* and may be polymorphic for 3 alleles. The most anodally migrating liver esterase is possibly monomorphic. The data from hemoglobin-$^{II}\alpha$ were included in our analysis, although 2 loci, and not alleles at 1 locus, are involved. Products of *HB-$^{II}\alpha$* were scored as absent, faint, or dark bands on gels stained with amido black. The locus represents a duplication of and is linked with a $^{I}\alpha$ gene, and apparently is segregating in Mendelian ratios in deer populations (Huisman et al. 1968, Taylor et al. 1972). Product of the $^{I}\alpha$ locus could not be distinguished by our techniques. Hemoglobin samples from SRP deer were compared against standards in the laboratory of Dr. T. H. J. Huisman (Medical College of Georgia).

Samples from 15 fetuses from 8 upland females also were analyzed. Bands of fetal samples were more weakly stained,

but scoring of allelic products was possible for all systems except *HB-β*. As found by Kitchen et al. (1967), the variable $^{II}\alpha$ minor band and a major band, which includes the delta-chains, occurred cathodal to adult samples. Data from fetuses were not included in statistical analyses.

## RESULTS

The following comparisons summarize the recent demographic history for the 2 SRP populations. The swamp herd was characterized by a changing demographic pattern, while the upland herd showed a stable age distribution and consistent age-specific survival and productivity. Since 1965, deer in the swamp reflected a declining, aging population with a significant shift toward older males, when the 3 age-classes were compared for 6 years ($P < 0.025$). These changes do not represent differential movement by males between the 2 areas, since losses are not compensated by gains in the other area for a particular age-class. However, the swamp population could have greater immigration and emigration rates, because continuous habitat extends north and south along the Savannah River.

It was evident that considerable differences in fetus-to-fawn survival and in fertility existed between the younger age-classes from the swamp and upland. Sex ratios among new fawns are influenced by the nutritional state of their mothers, the proportion of young females which breed (younger does produce more male offspring), differential susceptibility to hunting, and differential mortality (Robinette et al. 1957, Nixon 1971). Deficits of male fawns in the swamp suggested that the above factors differed between the 2 populations (Table 1). If vulnerability to hunting and similar biases were approximately equal between areas (Coe 1974:33), survivorship of fawns in 1970 and 1971 was in the order: female upland > female swamp > male upland > male swamp, as indicated in Table 1. Because comparisons of fitness are only valid within the same selective regime, survival of fawns relative to another class, adult females, was examined for each population (Dapson et al. in manuscript). Trends were the same as those from calculations of absolute survival, i.e., male fawns were at a disadvantage in both areas. Yearly variation in survivorship was much greater in the swamp, and survival of fawns was lowest in the swamp in 1971. A more severe reduction of male fawns was evident in the swamp, due primarily to lower productivity of young does, which normally produce excess numbers of males, and secondarily, to environmental factors such as flooding. Reproduction by fawns, revealed by lactation among yearling does, was consistently lower in the swamp through 1971 (Table 1). Female fawns in the upland showed a pregnancy rate 7 times greater and had 8 times more fetuses than those in the swamp.

**Table 1. Demographic history of South Carolina fawns from deer cohorts used for genetic analysis.**

| Locality and years | Percent male[a] fawns (±SD) | Fetus-to-fawn[b] survival (%) | | Fawn females breeding (%) |
|---|---|---|---|---|
| | | Male | Female | |
| Swamp | | | | |
| 1970 | 37.0 ± 6.6 | | | 8 |
| 1971 | 44.7 ± 8.1 | 29 | 48 | 7 |
| 1965–71 | 50.1 ± 5.7 | 47 | 57 | 14 |
| Upland | | | | |
| 1970 | 51.8 ± 3.2 | 43 | 64 | 45 |
| 1971 | 53.0 ± 2.9 | 42 | 56 | 42 |
| 1966–71 | 52.0 ± 3.3 | 47 | 65 | 44 |

[a] Percent males ($\bar{x} \pm$ SD) across years are weighted by yearly sample size.

[b] Absolute survival was calculated from age structure, age-specific fecundity and density estimates. No data were available for the swamp in 1969.

**Table 2. Observed proportions of heterozygotes (in parentheses) and allelic frequencies for polymorphic loci from 2 populations of white-tailed deer in South Carolina. For *HB-$^{II}\alpha$*, "I" indicates presence of gene duplication; all "100" alleles are omitted except for *HB-β* (see text). Superscript numbers show different sample sizes.**

| Loci and alleles | Populations, age-classes (years), and sample sizes: Upland 0.5 (*N* = 70) | Upland 1.5 (*N* = 20) | Upland 2.5 + (*N* = 20) | Upland Total | Swamp 0.5 (*N* = 36) | Swamp 1.5 (*N* = 24) | Swamp 2.5 + (*N* = 46) | Swamp Total |
|---|---|---|---|---|---|---|---|---|
| *ES-2* | (0.514) | (0.500) | (0.800) | (*0.564*) | (0.528) | (0.375) | (0.475) | (*0.462*) |
| 36 | 0.500 | 0.300 | 0.500 | *0.464* | 0.347 | 0.312 | 0.315 | *0.325* |
| *TRF* | (0.324)$^{71}$ | (0.400) | (0.600) | (*0.387*)$^{111}$ | (0.405)$^{37}$ | (0.417) | (0.356)$^{45}$ | (*0.387*) |
| 91 | 0.169 | 0.200 | 0.350 | *0.207* | 0.189 | 0.208 | 0.244 | *0.217* |
| 85 | 0.007 | | | *0.005* | 0.014 | | | *0.005* |
| *PGM-2* | (0.300) | (0.200) | (0.100) | (*0.245*) | (0.194) | (0.292) | (0.174) | (*0.208*) |
| 86 | 0.821 | 0.900 | 0.900 | *0.850* | 0.875 | 0.854 | 0.913 | *0.887* |
| 66 | | | | | 0.014 | | | *0.005* |
| *GOT-2* | (0.229) | (0.400) | (0.150) | (*0.245*) | (0.278) | (0.250) | (0.239) | (*0.255*) |
| −50 | 0.857 | 0.800 | 0.925 | *0.859* | 0.833 | 0.875 | 0.837 | *0.844* |
| *SDH* | (0.386) | (0.400) | (0.450) | (*0.400*) | (0.389) | (0.417) | (0.444)$^{45}$ | (*0.419*)$^{105}$ |
| 45 | 0.171 | 0.200 | 0.275 | *0.195* | 0.180 | 0.229 | 0.222 | *0.209* |
| 7 | 0.793 | 0.725 | 0.675 | *0.759* | 0.778 | 0.750 | 0.711 | *0.743* |
| −20 | | | | | 0.014 | | | *0.005* |
| *MDH-1* | (0.100) | (0.100) | (0.150) | (*0.109*) | (0.194) | (0.125) | (0.087) | (*0.132*) |
| 79 | 0.064 | 0.050 | 0.125 | *0.073* | 0.097 | 0.062 | 0.043 | *0.066* |
| *HB-$^{II}\alpha$* | (0.535) | (0.350) | (0.450) | (0.486) | (0.378)$^{37}$ | (0.375) | (0.356)$^{45}$ | (*0.368*) |
| I | 0.296 | 0.275 | 0.325 | *0.297* | 0.297 | 0.271 | 0.244 | *0.269* |
| *HB-β* | (0.391)$^{69}$ | (0.600) | (0.550) | (*0.459*)$^{109}$ | (0.432) | (0.417) | (0.400) | (*0.415*) |
| II | 0.203 | 0.325 | 0.300 | *0.243* | 0.243 | 0.229 | 0.233 | *0.236* |
| III | 0.732 | 0.650 | 0.600 | *0.693* | 0.716 | 0.750 | 0.756 | *0.740* |
| V | | | | | | | 0.011 | *0.005* |
| VII | 0.065 | 0.025 | 0.100 | *0.064* | 0.041 | 0.021 | | *0.019* |

Protein systems considered polymorphic ($P \geq 0.05$) and allelic frequencies are presented in Table 2. Banding patterns on gels were analogous to those described for *Peromyscus* by Selander et al. (1971), and similar genetic interpretations were inferred. A rare allele at the *LDH-2* locus was present in 6 individuals, and a single individual showed a possible additional allele at the *ES-2* locus. Use of eserine as an inhibitor suggested the probable existence of an additional esterase system with bands hidden by those of *ES-2*; however, patterns were too variable for clear interpretation. Minor alleles not present in the upland samples were detected at several loci in the swamp population. Two different female fawns were *PGM-2$^{86/66}$* and *SDH$^{7/-20}$* heterozygotes, while 1 male adult was a *HB-β$^{III/V}$* heterozygote.

The transferrin zymogram was confirmed by rivanol precipitation, and the pattern apparently corresponds to that shown by Miller et al. (1965:719). Their data indicate the presence of 2 alleles at this locus for deer from several localities in Iowa. The major allele was at frequencies of 0.81 and 0.71 in 1962 and 1963, respectively. The most anodal band of their 2-band and 3-band patterns probably represents subbanding by major polypeptides. At least 3 alleles occur in SRP deer; a male upland fawn and a female swamp fawn each were *TRF$^{100/85}$* heterozygotes. Seal and Erickson (1969:706) ob-

Table 3. Numbers of genotypes for 2 loci in deer from 2 South Carolina populations. Expected values (in parentheses) from a test for homogeneity are given for the esterase locus.

| Locus and genotypes | Upland | | Swamp | |
|---|---|---|---|---|
| | Females | Males | Females | Males |
| Esterase-2 | | | | |
| 100/100 | 17 (23.3) | 11 (14.9) | 31 (22.2) | 16 (14.6) |
| 100/36 | 41 (34.4) | 21 (22.1) | 29 (32.9) | 20 (21.6) |
| 36/36 | 9 (9.3) | 11 (6.0) | 4 (8.9) | 6 (5.8) |
| Hemoglobin-$\beta$ | | | | |
| II/II | 5 | 1 | 4 | 1 |
| III/III | 28 | 25 | 28 | 29 |
| II/III | 26 | 10 | 28 | 11 |
| III/V | 0 | 0 | 0 | 1 |
| II/VII | 1 | 4 | 1 | 0 |
| III/VII | 6 | 3 | 3 | 0 |

served a single fast band for transferrin in an enclosed herd of Minnesota deer (subbanding assumed).

Results for the hemoglobin loci can be compared with those of Harris et al. (1973:273) who gave data on the geographic distribution of hemoglobin variants in the southeastern U.S. One sample of 58 deer came from 2 South Carolina counties along the Savannah River immediately north of the SRP. Calculation of allelic frequencies from their Table 2 gives values of 0.47 ($\beta^{II}$), 0.46 ($\beta^{III}$), and 0.035 ($\beta^{IV \text{ and } VII}$). These differ considerably from the frequencies found in our samples, although their genotypic ratios were close to the expected Hardy-Weinberg proportions. Gene product of $^{II}\alpha$ was present in 67.2% of those deer compared with 50.5% of our samples. No comparison with the data of Miller et al. (1965) or Seal and Erickson (1969) is possible, but the $\alpha$-locus duplication is apparently present in Iowa and Minnesota deer populations.

No deviation from expected Hardy-Weinberg proportions of genotypes was observed at individual loci for the 2 populations. Tests of homogeneity were performed to compare genotypic frequencies in the 2 herds (Tables 2 and 3). Significant heterogeneity was detected for the *ES-2*, *HB-*$^{II}\alpha$ and *HB-*$\beta$ loci. Upland and swamp populations differed in proportions of the *ES-2* genotypes ($P < 0.01$). The upland herd also showed an excess of heterozygotes for the V and VII alleles of *HB-*$\beta$ as compared with the swamp herd ($P < 0.05$). Comparison of the 4 sex and habitat classes revealed excess $ES\text{-}2^{100}$ homozygotes among swamp females, excess $ES\text{-}2^{36}$ homozygotes among upland males, and excess heterozygotes among upland females ($P < 0.025$). For all deer combined, too many females were $HB\text{-}\beta^{II/III}$ heterozygotes and too few were $HB\text{-}\beta^{III}$ homozygotes as compared with the opposite situation for males ($P < 0.05$). Heterogeneity in genotypic proportions with respect to age was observed for *HB-*$^{II}\alpha$, where upland fawns had proportionately more heterozygotes than swamp fawns ($P < 0.025$) and upland adults ($P < 0.01$). Genetic heterogeneity was concurrent with other observed biological differences between the 2 herds and largely involved differences in proportions of heterozygotes.

Calculations of the average proportion of heterozygous loci per individual produced estimates of mean heterozygosity ($H$) in deer that are among the highest reported for a vertebrate species. Values derived from protein variation are commonly near 6% (Selander and Johnson 1973). The mean for 212 deer was 12.7%. Variable genic products were detected for 36% of the systems; no individual was heterozygous at more than 6 examined loci. Upland deer had an $H$ of 13.2%, while that of swamp deer was 12.2%. When the *HB-*$^{II}\alpha$ locus was excluded, the mean for both populations was 11.3% and

11.2%, respectively; one-third of the loci were polymorphic, and no individual was heterozygous at more than 5 loci.

## DISCUSSION

The demonstrated genetic heterogeneity within and between 2 adjacent deer populations suggests several potential applications of genic analysis in game management. Genetic data may indicate that the population requiring management practices is smaller than the management unit in use. Detection of local genetic differentiation of deer herds from multiple, geographically dispersed samples is possible by use of the *F*-statistics (Wright 1965, Workman and Niswander 1970). Thereby, genetic subdivision could be used as one criterion for designating the population subject to management. Considerable genetic heterogeneity may occur due to subdivision by breeding structure and distance. Little is known concerning subdivision within deer populations, but there is evidence of geographic variation. Using skull measurements and genetic distances, Rees (1969) found that genetic affinity was less between enclosed and neighboring deer populations than between some geographically distant groups. The data of Harris et al. (1973) suggest a W-E cline in frequencies of the V and VII alleles of *HB-β* with highest frequencies occurring in Mississippi and Louisiana. In contrast to the SRP deer, their sample within 160 km of the SRP contained the $\beta^{IV}$ allele and 17% more *HB-β* heterozygotes. Many existing deer herds began from restocking programs involving source populations that were hundreds of kilometers away. The geographic mosaic of gene pools created by restocking eventually loses its sharp boundaries, but the initial occurrence of rare alleles facilitates detection of migrants. Our observation of several rare alleles in the swamp population could indicate recent immigration. Migration rates can be estimated from initial and final gene frequencies of intermixed populations (Wallace 1968:79–81). Evidence of natural selection might be shown from variation in allele frequencies by the heterogeneity in apparent inbreeding coefficient either between generations or among loci across several populations (Lewontin and Krakauer 1973). These estimates require relatively large, replicate samples; however, such data can be generated under conditions of most controlled hunting.

Demonstrated correlations between demographic and genetic differences do not establish a cause-effect relationship. While the present data are insufficient for detailed treatments, several problems can be suggested for examination in further studies. Smith et al. (1975) reviewed the evidence that different degrees of genetic variability (heterozygosity) result in different reproductive potentials and behavioral attributes. Among SRP deer, upland does differed from swamp does in genotypic proportions for *ES-2* and *HB-β* and in reproductive performance. Certain introduced or penned deer populations could be useful for testing the possible relationship between genotype and reproduction. Other effects cannot be ignored, however. Differences in available diet may have existed between the swamp and upland habitats on the SRP (Urbston 1976). Possible influence of genotype on behavioral aspects of sex-related mortality should be investigated. Male fawns are more active than females, and thus, are more prone to accidents and predation (Jackson et al. 1972:269). Certain loci should receive increased attention in future investigations. Among the sex, age, and area categories, notable contributions of heterozygotes to values of *H*

were made by transferrin in the swamp, by both hemoglobin systems in the upland and by *HB-β* in young swamp females. Secondary physiological consequences are known in deer for the $\beta^{V}$ and $\beta^{VII}$ alleles which preclude sickling of stressed red cells and may have other effects (Kitchen et al. 1967).

## LITERATURE CITED


COE, R. J. 1974. The causes of bias in white-tailed deer kill data. M.S. Thesis. Virginia Polytechnic Institute and State University. 84pp.

GAINES, M. S., AND C. J. KREBS. 1971. Genetic changes in fluctuating vole populations. Evolution 25:702–723.

GILLESPIE, J., AND K. KOJIMA. 1968. The degree of polymorphism in enzymes involved in energy production compared to that in nonspecific enzymes in two *D. ananassae* populations. Proc. Nat. Acad. Sci. U.S.A. 61:582–585.

HARRIS, M. J., T. H. J. HUISMAN, AND F. A. HAYES. 1973. Geographic distribution of hemoglobin variants in the white-tailed deer. J. Mammal. 54:270–274.

HUISMAN, T. H. J., A. M. DOZY, AND M. H. BLUNT. 1968. The hemoglobin heterogeneity of the Virginia white-tailed deer: a possible genetic explanation. Arch. Biochem. Biophys. 127:711–717.

JACKSON, R. M., M. WHITE, AND F. F. KNOWLTON. 1972. Activity patterns of young white-tailed deer fawns in South Texas. Ecology 53:262–270.

KITCHEN, H., F. W. PUTNAM, AND W. J. TAYLOR. 1967. Hemoglobin polymorphism in white-tailed deer: subunit basis. Blood 29:867–877.

LEWONTIN, R. C., AND J. KRAKAUER. 1973. Distribution of gene frequency as a test of the theory of the selective neutrality of polymorphisms. Genetics 74:175–195.

MANLOVE, M. N., J. C. AVISE, H. O. HILLESTAD, P. R. RAMSEY, M. H. SMITH, AND D. O. STRANEY. 1975. Starch gel electrophoresis for the study of population genetics of white-tailed deer. Proc. Southeast. Assoc. Game Fish Comm. 29:392–403.

MILLER, W. J., A. D. HAUGEN, AND D. J. ROSLIEN. 1965. Natural variation in the blood proteins of white-tailed deer. J. Wildl. Manage. 29:717–723.

NIXON, C. M. 1971. Productivity of white-tailed deer in Ohio. Ohio J. Sci. 71:217–225.

REDFIELD, J. A., F. C. ZWICKEL, J. F. BENDELL, AND A. T. BERGERUD. 1972. Temporal and spatial patterns of allele and genotype frequencies at the *Ng* locus in blue grouse (*Dendragapus obscurus*). Can. J. Zool. 50:1657–1662.

REES, J. W. 1969. Morphologic variation in the cranium and mandible of the white-tailed deer (*Odocoileus virginianus*): A comparative study of geographical and four biological distances. J. Morphol. 128:95–112.

ROBINETTE, W., J. GASHWILER, J. LOW, AND D. JONES. 1957. Differential mortality by sex and age among mule deer. J. Wildl. Manage. 21:1–16.

SEAL, U. S., AND A. W. ERICKSON. 1969. Hematology, blood chemistry and protein polymorphisms in the white-tailed deer (*Odocoileus virginianus*). Comp. Biochem. Physiol. 20:695–713.

SELANDER, R. K., AND W. E. JOHNSON. 1973. Genetic variation among vertebrate species. Ann. Rev. Ecol. Syst. 4:75–91.

———, M. H. SMITH, S. Y. YANG, W. E. JOHNSON, AND J. B. GENTRY. 1971. Biochemical polymorphism and systematics in the genus *Peromyscus*. I. Variation in the old-field mouse (*Peromyscus polionotus*). Studies in Genetics. VI. Univ. Texas Publ. 7103:49–90.

SMITH, M. H., C. T. GARTEN, JR., AND P. R. RAMSEY. 1975. Genic heterozygosity and population dynamics in small mammals. Pages 85–102 *in* C. L. Markert, ed., Isozymes, Vol. IV, genetics and evolution. Academic Press, New York.

———, R. K. SELANDER, AND W. E. JOHNSON. 1973. Biochemical polymorphism and systematics in the genus *Peromyscus*. III. Variation in the Florida deer mouse (*Peromyscus floridanus*), a Pleistocene relict. J. Mammal. 54:1–13.

TAYLOR, W. J., C. W. EASLEY, AND H. KITCHEN. 1972. Structural evidence for heterogeneity of two hemoglobin α chain gene loci in white-tailed deer. J. Biol. Chem. 247:7320–7324.

URBSTON, D. F. 1967. Herd dynamics of a pioneer-like deer population. Proc. Southeast. Assoc. Game Fish Comm. 21:42–57.

———. 1972. Status of Savannah River Plant deer herd: Herd dynamics and deer hunts through 1971. Natl. Tech. Inf. Serv. (SRO-154):1–13.

———. 1976. Descriptive aspects of two fawn populations as delineated by reproductive differences. Ph.D. Thesis. Virginia Polytechnic Institute, Blacksburg, Va. 104pp.

WALLACE, B. 1968. Topics in population genetics. W. W. Norton and Company, Inc., New York. 481pp.

WORKMAN, P. L. AND J. D. NISWANDER. 1970. Population studies on Southwestern Indian tribes. II. Local genetic differentiation in the Papago. Am. J. Hum. Genet. 22:24–49.

WRIGHT, S. 1965. The interpretation of population structure by F-statistics with special regard to systems of mating. Evolution 19:395–420.


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