GENETIC SUBDIVISION IN A HERD OF WHITE-TAILED DEER AS DEMONSTRATED BY SPATIAL SHIFTS IN GENE FREQUENCIES

by
MICHAEL N. MANLOVE[1]
Department of Fisheries and Wildlife
Michigan State University
East Lansing, Michigan 48824

MICHAEL H. SMITH
Savannah River Ecology Laboratory
Drawer E
Aiken, South Carolina 29801

HILBURN O. HILLESTAD
Institute of Natural Resources
University of Georgia
Athens, Georgia 30602

SUSAN E. FULLER
Department of Fisheries and Wildlife
Oregon State University
Corvallis, Oregon 97331

PAUL E. JOHNS
Savannah River Ecology Laboratory
Drawer E
Aiken, South Carolina 29801

DONALD O. STRANEY
Department of Zoology
University of California at Berkeley
Berkeley, California 94720

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ABSTRACT

Allele frequency data for the β-hemoglobin locus from 452 white-tailed deer (Odocoileus virginianus) *from the Savannah River Plant were examined for spatial subdivision of the herd. The usefulness of electrophoretic techniques to gather genetic information for analysis of spatial subdivision is demonstrated. Significant spatial heterogeneity was found; thus, the herd probably consists of more than one functional population. The potential use of these populations as independent management units is discussed.*

The management unit is an extremely important concept in wildlife management. Its operational definition is seldom based on functional characteristics of the population(s) included. Ideally a population should form the basis of a management unit if it has functional characteristics (e.g., reproductive rate) which differ from those of adjacent populations and are of importance in determining population number and dynamics. Spatial boundaries of management units should, wherever practical, be based on functional characteristics of the populations of interest. The question of recognizing and defining a population then becomes of utmost importance.

[1]Reprint requests should be sent to M. H. Smith, Savannah River Ecology Laboratory, Drawer E, Aiken, S.C. 29801.

One approach to this problem is to define a population as a breeding unit and to use the spatial distribution of alleles to help identify populations. Animals in the same breeding population should be similar genetically and statistical comparisons of allele frequencies between subpopulations should not reveal any significant differences. Spatial heterogeneity in allele frequencies then can be used to identify local populations for further study and possible designation as management units.

Our objective in this paper is to examine allele frequency data for the β-hemoglobin locus in white-tailed deer from one local area to determine the existence and extent of subdivision within a herd. Emphasis will be placed on the method of analysis since it can be theoretically applied to all fish and wildlife species. Allele frequency data can be easily obtained through the use of electrophoretic techniques making this approach practical for a wide variety of species (Manlove et al., 1976). With a relatively large locally available sample, the white-tailed deer was chosen from among several species to illustrate the utility of this approach.

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STUDY AREA

The Savannah River Plant (SRP) site, near Aiken, South Carolina borders the northern bank of the Savannah River and covers nearly 800 square kilometers of limited access property. Most of the site currently supports agricultural pine stands interspersed with a network of power line clearings, old-field plots in various stages of succession, and bottomland hardwoods along the creeks and river. The area's geologic and recent history as well as the local climate and biota were described by Langley and Marter (1973).

The complete area is partitioned into 50 wildlife compartments managed by the U.S. Forest Service. The definition of these compartments is arbitrary relative to the deer population, but based on practical considerations (e.g., position of roads). The precise arrangement of these compartments is available from the U.S. Forest Service, on the SRP. Each of these compartments is potentially a management unit but in reality, management is practiced on a larger scale. Public deer hunts are operated by the Forest Service with deer harvested from at least 40 of these compartments. Annual harvests have ranged from 1,200 to 1,500 animals since 1973.

Urbston (1967) discussed the population dynamics of the SRP herd with data obtained through 1966. The current population which occupies virtually all of the site apparently grew within a decade from a small source of animals restricted to the wet lowlands prior to limited public access in the early 1950's. Data from 1965-1971 suggested that swamp and upland deer exhibited different demographic characteristics with swamp deer having lower reproductive success (Urbston 1972). Thus substantial differences exist in demographic characteristics over a limited area and can be used in a meaningful management program.

MATERIALS AND METHODS

Blood samples were collected from some of the deer harvested September through December of 1974 by hunters on the Savannah River Plant. Deer from thirty-five compartments were sampled, permitting a representative survey of deer from 70 percent of the plant site. A total of 452 deer of all postnatal age classes and both sexes are used in this analysis.

Blood was collected in heparinized capillary tubes, separated into red cell and plasma components by centrifugation and subjected to horizontal starch gel electrophoresis. Results reported here are for gene frequency data at the β-hemoglobin locus assayed using red cell hemolysate. Procedural details for collection, storage and electrophoresis of blood are explained more fully by Manlove et al. (1976).

To assess the degree and nature of genetic subdivision in the SRP herd, three levels of comparison were made by partitioning the total SRP sample into smaller units and calculating allele frequencies for each unit. The first level compares swamp vs upland deer with samples from 25 wildlife compartments representing most of the SRP. We define "swamp" to consist of six adjacent compartments (numbers 29, 35, 43, 44, 48 and 49), in the lowland area bordering the Savannah River along the southern periphery of the SRP (see Urbston 1972). The second level compares seven individual wildlife compartments from which sample sizes of 30 or more deer were obtained in the swamp and upland areas. The third level compares gene frequencies within and between two adjacent swamp compartments (numbers 44 and 48). Compartment 44 was divided in half by a transect parallel to the Savannah River to measure intracompartmental differences. This compartment had the largest sample size (N = 45) of any compartment on the SRP.

Spatial differences in gene frequency were tested for significance by Chi-square analyses. The correlation between alleles within areas relative to that expected for the total population was determined by calculating F_{ST} for each hierarchal level of subdivisions (Wright 1965; Figs. 1-2). These values specify the amount of inter-area variance in gene frequencies relative to the weighted mean frequencies in the total populations, such that for a locus with two alleles, $F_{ST} = \delta^2$ where δ^2 is the between area frequency variance and $\bar{p}$ and $\bar{q}$ are the weighted mean frequencies of the alleles across areas. F_{ST} varies between zero and one with zero resulting from complete equality of allele frequencies between areas. There are four alleles of β-hemoglobin (Hb-β) appearing on the site, and the data for the two rare alleles (frequency $\leq$ .05), were pooled with those of the most common allele to simplify analyses.

RESULTS

Of six allelic variants for β-hemoglobin reported in southeastern deer (Harris et al., 1973), only the Hb-β^2, β^3 and β^7 alleles occurred in a frequency greater than .005 in the herd, with the β^5 allele present but extremely rare. The β^7 allele was also relatively rare (frequency $\cong$ .05) with the β^3 allele being the most common (frequency > 0.5).

The frequencies of the β^2 allele in two primary regions on the plant; swamp and upland, were .272 (N = 133) and .233 (N = 319), respectively. The difference is not significant, and a relatively homogeneous distribution of these alleles between swamp and upland deer is suggested at this level of comparison (F_{ST} = .0019; P > .25).

Upon comparing individual wildlife compartments considerable spatial heterogeneity in gene frequency is revealed (Fig. 1). Sample sizes for the seven compartments identified in Fig. 1 range from 30 to 45. Compartment 44 is in the swamp and the remaining six compartments represent subdivisions of the upland sample. The between area variance in gene frequencies was relatively high (F_{ST} = .041, X^2 = 18.9, and P = .02) but somewhat less than frequency shifts found at this locus between deer populations from different regions throughout the southeast (Smith et al., 1976). F_{ST} values obtained for populations of other mammalian species range from .00067 for humans (Japanese mainland) to .174 for house mice in barns (as summarized in Selander and Kaufman, 1975).

The swamp sample was further subdivided to illustrate the extent of spatial heterogeneity within certain compartments (Fig. 2). Sample sizes for *a*, *b* and *c* in Fig. 2 were 17, 28 and 20 respectively. While samples in areas *b* and *c* had similar gene frequencies, those in areas *a* and *b* within the same hunt compartment had a two-fold difference in frequency of the β^2 allele. The heterogeneity in allele frequency within compartment 44 was relatively high (F_{ST} = .025) but with the small sample sizes the differences in allele frequencies were not significant (P > .25). We restricted our analysis at this level to only one compartment (number 44) because of inadequate sample size within the others. An analysis where every hunt compartment could be divided into smaller units would have been ideal, but would have required considerably more than 452 deer. Despite the problems with sample size, indications are that the within and between compartment heterogeneity may be comparable (F_{ST} = .025 vs .041, respectively).

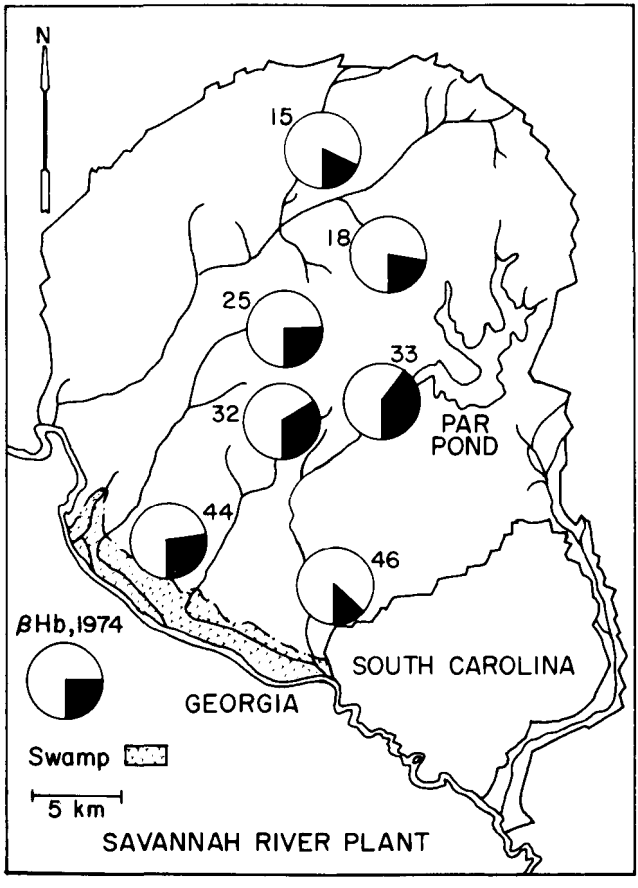

Figure 1. Frequency of the hemoglobin -β^2 allele in white-tailed deer sampled from seven wildlife compartments designated by compartment number within the Savannah River Plant. Frequencies are expressed as proportions of a circle.

DISCUSSION

The idea that populations may be genetically subdivided across small geographic areas is not new (Wright 1943). Spatial subdivision apparently is the rule rather than the exception for vertebrates (Smith et al. in press). For example, there may be several populations of house mice (*Mus musculus*) in a barn (Selander 1970). Other documented examples of spatial heterogeneity include populations of deer mice (*Peromyscus* sp.; Selander et al. 1971; Smith et al. 1973), blue grouse (*Dendragapus obscurus*, Redfield 1974) and sunfish (*Lepomis* sp.; Avise and Smith 1974 a,b). Although deer are large and appear to have a high dispersal capacity, their populations are also genetically subdivided through space as demonstrated by our data and those of Harris et al. (1973) and Smith et al. (1976).

Similar analyses with other loci in deer will probably reveal even greater spatial subdivision as has been found in other species. Temporal heterogeneity in allele frequencies should also be expected (Krebs et al. 1973; Smith et al. in press), but our data were taken

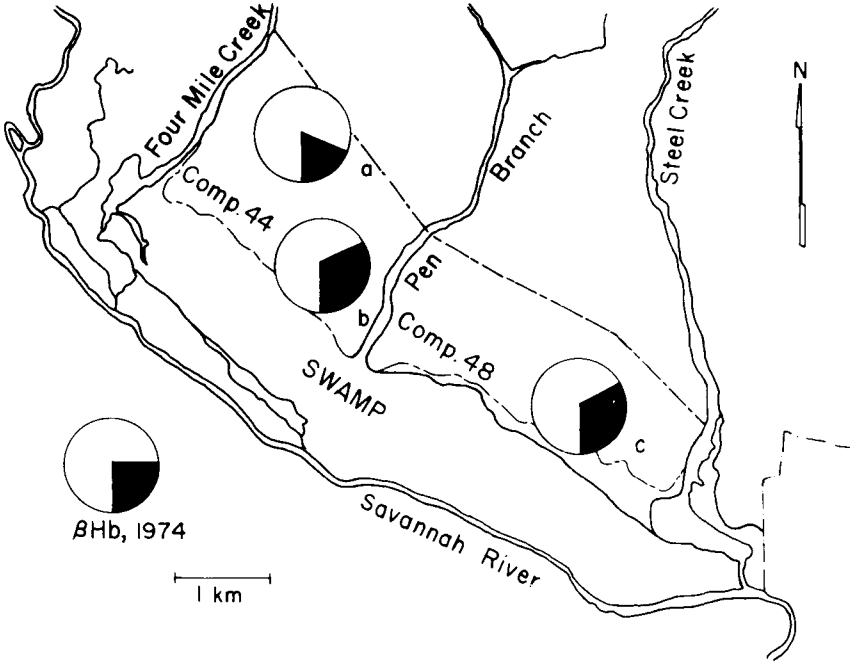

Figure 2. Frequency of the hemoglobin -β^2 allele in white-tailed deer from two wildlife compartments from the swamp area of the Savannah River Plant. Frequencies are expressed as proportions of a circle.

from a single year and cannot be used to test for this effect. Deer populations should be viewed as dynamic units on relatively small spatial and temporal scales.

The potential causes of this subdivision are worth considering. Differential selection in a heterogeneous environment could theoretically cause the observed pattern (Levins 1969). There are no data to support or even suggest this possibility in white-tailed deer, and it is difficult to understand how selection might operate on such a fine scale with such a large animal. The social organization of white-tailed deer probably limits the free exchange of individuals between breeding groups. Limited dispersal leads to isolation by distance (Wright 1943) and maintenance of localized breeding units (Wright 1951). Founder effect and drift can result in significant differences in allele frequencies through space. Under these circumstances the effective population size may be small when measured over relatively short time intervals, and the cause of subdivision stochastic. The effects on the animals within the local units may still be profound with respect to their individual fitnesses.

Small populations may form the basis of meaningful management units. For this to be true, they must have temporal stability and interpopulational differences in important demographic characteristics. Although we have demonstrated genetic subdivision within the Savannah River Plant herd, information concerning the latter two conditions is lacking. Once the subdivisions are identified then appropriate data can be gathered to determine their usefulness as management units.

The demonstration of genetic subdivision through space does not identify the exact genetic populations, although it substantiates their existence. Arbitrary subdivision of the samples does not result in a precise definition of local breeding populations. A technique is needed to cluster individuals of similar genetic characteristics into temporal

and spatial aggregates. We can expect the data requirements for this approach to be rigorous and to include intensive sampling efforts.

Despite these difficulties, it is clear that the Savannah River Plant deer herd is genetically subdivided. The scale of comparison is important to the demonstration of this subdivision. Treating the herd as a single population is inadequate. The subsequent association of pertinent demographic differences with the observed spatial genetic heterogeneity is the challenge for the future and should allow specific recommendations for realistically defining meaningful management units.

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