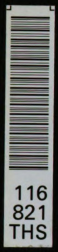


This is to certify that the

thesis entitled

GENETIC SIMILARITY AMONG CONTIGUOUS AND ISOLATED POPULATIONS OF WHITE-TAILED DEER IN MICHIGAN

presented by

Michael N. Manlove

has been accepted towards fulfillment
of the requirements for

MASTER OF SCIENCE degree in Fisheries & Wildlife

Harold H. Prince
Major professor

Date 8-7-79

O-7639

# GENETIC SIMILARITY AMONG CONTIGUOUS AND ISOLATED POPULATIONS OF WHITE-TAILED DEER IN MICHIGAN

By

Michael N. Manlove

A THESIS

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

MASTER OF SCIENCE

Department of Fisheries and Wildlife

1979

## ABSTRACT

GENETIC SIMILARITY AMONG CONTIGUOUS AND ISOLATED POPULATIONS OF WHITE-TAILED DEER IN MICHIGAN

By

Michael N. Manlove

Genetic indices were compared among white-tailed deer (Odocoileus virginianus) from five areas in the Upper and Lower Peninsulas of Michigan. Using starch-gel electrophoresis of muscle tissue extracts, protein phenotypes were observed for eleven monomorphic and nine polymorphic loci. Significant spatial subdivision among areas was observed in gene frequencies for three loci. Mean individual heterozygosity (H) estimates averaged about nine percent and did not vary significantly among areas. Genetic distance (Nei, 1972) was higher between eastern and western Upper Peninsula populations (D=0.008) than among Lower Peninsula populations ($\bar{D}$=0.002). Distance between Upper and Lower Peninsula populations separated by the Mackinaw Strait was also relatively high (D=0.008). This conforms to descriptions of morphological disimilarity between Upper and Lower Peninsula deer made by other investigators.

## ACKNOWLEDGEMENTS

I wish to thank my graduate committee members, Drs. Harold H. Prince, Rollin H. Baker and Richard Hill for their critical review and comments on the manuscript. Glenn Dudderer and Dave Arnold provided helpful information about Michigan deer and relevant source material. I am especially grateful to John Stuht of the Rose Lake Wildlife Research Station who arranged and coordinated the collection efforts through cooperation of the Michigan Department of Natural Resources. Michael H. Smith graciously permitted my use of laboratory space and facilities at the Savannah River Ecology Laboratory. Rose Manlove typed the manuscript and provided valuable editorial assistance. During this research I was supported by a research assistantship funded by the Agricultural Experiment Station, Michigan State University.

TABLE OF CONTENTS

## LIST OF TABLES

## LIST OF FIGURES

# INTRODUCTION

Appreciation of geographic variation among populations has increased considerably since Darwin's time. Methods of observation and statistical analyses of variation have also become more sophisticated. The amount of genetic variation among individuals within and between populations has, in the past decade, been recognized as much greater than previously suspected. The relationship of genetic variation to the environment in which individuals grow and reproduce, and the ambiguous adaptive significance of such variation remain, however, as problematic obstacles to a synthesis of theories of population biology and the evolution of complex adaptations. These also severely challenge our efforts to adequately manage species and their habitats.

Studies of genetic variation in mammals have made extensive use of electrophoresis and histochemical staining methods to observe variation in specific protein isozyme phenotypes. A great variety of species have been so studied, although most research has dealt with small mammals (see Smith et al. 1978). Several studies documenting genetic variation in mammals have had a systematic and taxonomic concern, and therefore confront us with questions about the rate at which protein isozymes evolve (e.g., Avise et al. 1974; Avise, 1976; Zimmerman et al. 1978).

Given the variety of metabolic functions of various enzymes and the technical limits to detecting various forms of genetic variation, the problems with a locus-by-locus approach to explaining patterns of variation are obviously enormous. Therefore, Smith et al. (1975), for example, have emphasized the value of measures of overall variability in the genome (i.e., average individual heterozygosity estimates) for studying the role of genetic variation in population processes.

Research on genetic variation at the population level has mostly involved descriptive comparisons of natural populations from different geographic or biotic regions, communities or local habitats. Temporally replicated comparisons are scarcer in the literature. Experimental manipulations of laboratory and natural populations are only recently gaining momentum, particularly for mammals and other vertebrates. When well designed, general surveys of genetic variation are useful and necessary. Our ability to integrate the developing theories of population biology with practical concerns for managing our environment, including our wildlife resources, however, will require controlled experiments with the species and habitats concerned.

The application of genetics information to ideas and programs of wildlife management is in its infancy. The potential for this application and a review of relevant research efforts were presented by Smith et al. (1976). The results of such efforts imply that genetics cannot be

safely ignored in planning management strategies. They also expose the need for further descriptive and experimental studies to better understand any purposeful or inadvertant effects of humans on the genetic structure of wildlife populations.

Published studies of genetic variation in large mammals are limited, so far, to only a few species. Long term studies concerned with genetic correlates to concurrent population dynamics have concentrated on one species, the white-tailed deer in South Carolina (Ramsey et al. 1979; Smith et al. in press). This research has shown that (a) significant spatial differences in gene frequencies may occur among local groups, (b) local genetic subdivision is dynamic in time within and between sex and age groups, (c) average individual heterozygosity (H) is positively correlated with reproductive success, and (d) prenatal selection operates measurably for at least some enzyme phenotypes.

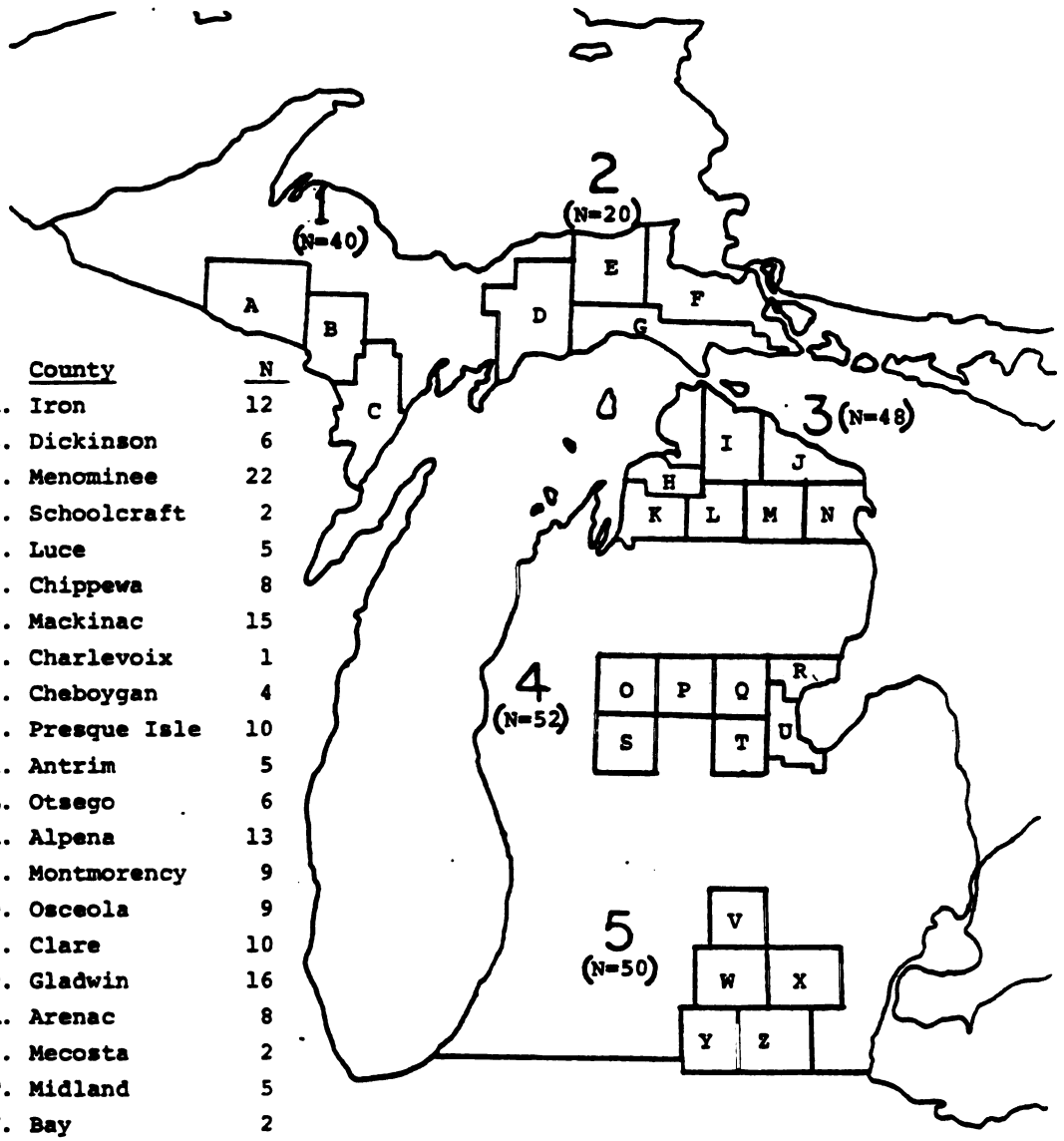
As the relationship of genetic structure to the demography of these populations becomes better understood and documented we will then be in a better position to compare deer populations inhabiting different environments and subject to different management strategies.

The present study concerns a point-in-time observation of genetic variation among deer populations in Michigan based on biochemical indices. My objective was to use observations of protein variation in deer to estimate the

amount of variability and genetic distance between contiguous and relatively isolated populations within the State. It is hoped that this will provide a basis for future research that is cognizant of potential genetic differences that may exist among deer populations in Michigan.

## MATERIALS AND METHODS

Male deer (N=210) of different ages were sampled from five pre-selected areas in the western and eastern Upper Peninsula and the northern, central and southern Lower Peninsula of Michigan during the fall 1977 hunting season. These samples represented geographically isolated as well as potentially contiguous populations. Collection localities are specific to the county where the deer were killed. Due to sample size constraints, each of the areas used for comparison included several adjacent counties (Figure 1). The areas described are not based on preconceptions about the extent or distribution of functional, genetically cohesive populations. An effort was made to sample areas of comparable size, similar distance apart, and representative of the geographic extent of the state including major habitat differences. A few additional samples were obtained from road-killed deer from across the state in Spring, 1977. Results for these samples are included in the list of isozymes surveyed (Table 1), but the frequencies of variable alleles observed for these deer are not included in the area comparisons.




| County | N |
|---|---|
| A. Iron | 12 |
| B. Dickinson | 6 |
| C. Menominee | 22 |
| D. Schoolcraft | 2 |
| E. Luce | 5 |
| F. Chippewa | 8 |
| G. Mackinac | 15 |
| H. Charlevoix | 1 |
| I. Cheboygan | 4 |
| J. Presque Isle | 10 |
| K. Antrim | 5 |
| L. Otsego | 6 |
| M. Alpena | 13 |
| N. Montmorency | 9 |
| O. Osceola | 9 |
| P. Clare | 10 |
| Q. Gladwin | 16 |
| R. Arenac | 8 |
| S. Mecosta | 2 |
| T. Midland | 5 |
| U. Bay | 2 |
| V. Ingham | 3 |
| W. Jackson | 43 |
| X. Washtenaw | 1 |
| Y. Hillsdale | 2 |
| Z. Lenawee | 1 |

Figure 1. Counties in Michigan from which deer were collected in 1977. Five sample areas of combined counties used for comparison are designated on the map. The sample distribution among counties is given with the list of counties in the key.

TABLE 1. Enzymes and general proteins observed in muscle tissue from deer in Michigan.

| Protein | Abbr. | Allele Designations* | | | |
|---|---|---|---|---|---|
| 6-Phosphogluconate dehydrogenase | (6-PGD) | | 100 | 64** | |
| Malic enzyme-1 | (ME-1) | 128 | 100 | | |
| ME-2 | | 127 | 100 | | |
| Malate dehydrogenase-1 | (MDH-1) | 120** | 100 | *** | |
| MDH-2 | | | 100 | | |
| Lactate dehydrogenase-1 | (LDH-1) | *** | 100 | *** | |
| LDH-2 | | *** | -100 | -80 | |
| Glutamate oxaloacetate transaminase-1 | (GOT-1) | | 100 | 75 | |
| GOT-2 | | | -100 | -70 | |
| Esterase-2 | (ES-2) | 107 | 100 | 86 | 36 |
| Mannose phosphate isomerase | (MPI) | | 100 | 82 | 64** |
| Phosphoglucomutase-2 | (PGM-2) | 133** 104 | 100 | 87 | |
| α-Glycerophosphate dehydrogenase-2 | (α-GPD-2) | 112** | 100 | 83 | |
| Albumin | (Alb) | 104** | 100 | | |
| Protein-2 | (Pt-2) | | 100 | | |
| Protein-3 | (Pt-3) | | 100 | | |
| Creatine Kinase | (CK) | | 100 | | |
| Protein-5 | (Pt-5) | | 100 | | |
| Phosphoglucose isomerase-1 | (PGI-1) | | 100 | | |
| PGI-2 | | | 100 | | |

* Migration distance relative to that of the common allele designated as 100 (cathodal migration) or -100 (annodal migration) for southeastern deer as described by Smith et al. (in press).

** Allele not observed in southeastern deer.

*** Allele observed in southeastern deer, but not in Michigan.

Muscle tissue for electrophoresis was obtained from deer brought to centralized checkpoints by hunters. Tissue samples were frozen and stored at -10°C. for up to 112 days until use. Fluid extracts of muscle tissue were subjected to horizontal starch gel electrophoresis according to the methods described by Kristjansson (1963) and Selander et al. (1971). Buffer systems used were as described by Selander et al. (1971), with minor modifications as described by Manlove et al. (1976).

Enzymes and non-enzymatic proteins were identified by substrate-specific staining methods as described by Selander et al. (1971), with the exception of creatine kinase, which was stained with two percent napthol blue black in fixing solution on the same gels used to identify albumin and other general proteins. Twenty proteins encoded by 20 loci were examined for each individual (Table 1). Individuals for which any of the 20 proteins could not be scored were excluded from analyses. Patterns of electrophoretic variation in proteins from white-tailed deer have been illustrated and described elsewhere (Manlove et al. 1976 ; Smith et al. in press).

Gene frequency and average individual heterozygosity estimates (H) were calculated from direct counts of the observed electrophoretic phenotypes. H is the proportion of observed loci that are heterozygous in the average individual of a population. The gene frequencies and heterozygosity values (h) for specific loci observed in each area

were compared with those predicted by Hardy-Weinberg assumptions using a Chi-square goodness-of-fit test.

To measure similarities between populations I have used Nei's (1972) index of identity. The normalized identity between populations at the $j^{th}$ locus is defined as

$$I_j = \Sigma x_i y_i \Big/ \left(\Sigma x_i^2 \, \Sigma y_i^2\right)^{1/2}$$

where $x_i$ and $y_i$ are the frequencies of the $i^{th}$ allele in populations x and y. The mean genic identity over all loci is

$$I = J_{xy} \Big/ \left(J_x J_y\right)^{1/2}$$

where $J_{xy}$, $J_x$, and $J_y$ are means of $\sum_1^j x_i y_i$, $\sum_1^j x_i^2$, and $\sum_1^j y_i^2$, respectively. This quantity is unity when the two populations have the same alleles in identical frequencies and is zero when they have no alleles in common. The genetic distance as reported in this paper between x and y is then defined as

$$D = -\log_e I$$

which may be considered an estimate of the accumulated number of gene substitutions per locus if the rate of gene substitution is the same for all loci (Nei, 1972).

The degree of heterogeneity among populations can also be expressed by means of an F statistic, $F_{ST}$ (Wright,

1965), which gives the ratio of the actual variance in gene frequency among populations to the overall frequency averaged across populations.

That is,

$$F_{ST} = \sigma_p^2 / \overline{pq}$$

where $\sigma_p^2$, $\bar{p}$, and $\bar{q}$ are the variance and weighted mean frequencies. $F_{ST}$ can also be defined as the correlation between random gametes within subpopulations relative to the ga etic array of the total population. The significance of spatial differences in gene frequency was tested by a $\chi^2$ analysis of observed and expected values based on a contingency table of alleles across five areas for each locus. A .05 confidence level was used to define statistical significance. For ease of computation I have combined the two rarest alleles in these analyses for loci having three alleles.

## RESULTS AND DISCUSSION

Six of the polymorphic loci had alleles not previously described for deer (Table 1). Those loci which had four alleles (Es-2 and PGM-2), also tend to be most variable in populations in the southeastern U. S. (Smith et al. in press). Fewer alleles were observed for both LDH loci in Michigan deer than in the southeastern U. S. (Smith et al.

in press). Two proteins, B-hemoglobin and sorbitol dehydrogenase, which are highly variable in South Carolina deer, could not be analyzed from muscle tissue used in this study. The analysis of a few blood samples from road-killed deer suggests that the predominant alleles for B-hemoglobin (Hb-$B^{II}$ and Hb-$B^{III}$) found in South Carolina (Manlove et al. 1976), are also common in Michigan. These alleles also occur in high frequency in the eastern coastal states at least as far north as Maryland (Harris et al. 1973). Transferrin from plasma samples of Michigan (Upper Peninsula) deer is not variable. One individual from the Upper Peninsula was heterozygous at the Albumin locus. The gene and genotype frequencies calculated for polymorphic loci in deer from each area in Michigan did not differ significantly from the distributions expected for Hardy-Weinberg equilibrium.

Forty-five percent of the observed loci were polymorphic. This is similar to values obtained for southeastern deer populations by Smith et al. (in press). Estimates of H did not vary significantly among any areas in Michigan and averaged about nine percent (Table 2). Previous estimates of H for three areas in Georgia and five in South Carolina ranged from 4.9 to 9.2 percent and significant differences were found between areas in both states (Smith et al. in press).

Estimates of H for deer in Michigan and the southeastern U. S. are among the highest yet observed in a large mammal species. Values reported for populations of polar bears (Larson, in press), black bears (Manlove et al. in press), chimpanzees (King and Wilson, 1975), and other North American

TABLE 2. Mean heterozygosity (H) estimates for deer in Michigan.

| Area | H*(±s.e.) | H**exp. |
|---|---|---|
| 1 | 0.0895(±0.0073) | 0.1013 |
| 2 | 0.0925(±0.0115) | 0.0824 |
| 3 | 0.0896(±0.0080) | 0.0844 |
| 4 | 0.0909(±0.0095) | 0.0799 |
| 5 | 0.0750(±0.0082) | 0.0796 |

* The proportion of loci heterozygous in the average individual of a population.

** The mean of heterozygosity values expected for each locus based on observed gene frequencies.

ungulates (Baccus et al. in press) are all under five percent. Humans average about 6.7 percent (Harris and Hopkinson, 1972).

Genetic differences between areas are demonstrated by significant spatial shifts in gene frequencies at three loci (MPI, Es-2 and GPD; Figs. 2, 3 and 4). At the MPI locus (Fig. 2), the most common allele ($Mpi^{100}$) in Lower Peninsula populations is significantly less frequent in both the western and eastern Upper Peninsula. A third allele, ($Mpi^{64}$), present in the Upper Peninsula, is absent in all Lower Peninsula samples. This allele is apparently absent in deer from the Savannah River Plant in South Carolina (Smith et al. in press). The MPI locus has not, however, been studied in other populations in the southeastern U. S. Three alleles at the Es-2 locus in Michigan deer (Fig. 3) have also been observed in South Carolina populations. The $Es\text{-}2^{107}$ allele was extremely rare in deer in the Michigan Upper Peninsula but more common in deer throughout the Lower Peninsula. The distribution of two alleles for GPD are presented in Figure 4. The $Gpd^{112}$ allele is rare in the southern Lower Peninsula, relatively common in the western portion of the Upper Peninsula and absent in deer from the eastern Upper Peninsula and the northern half of the Lower Peninsula. This allele has not been observed in deer in the southeastern U. S.

The $F_{ST}$ values listed in Table 3 depict the relative contributions of specific loci to genetic subdivision among various sample area combinations. There is considerable variation in $F_{ST}$ among loci for any combination of areas.

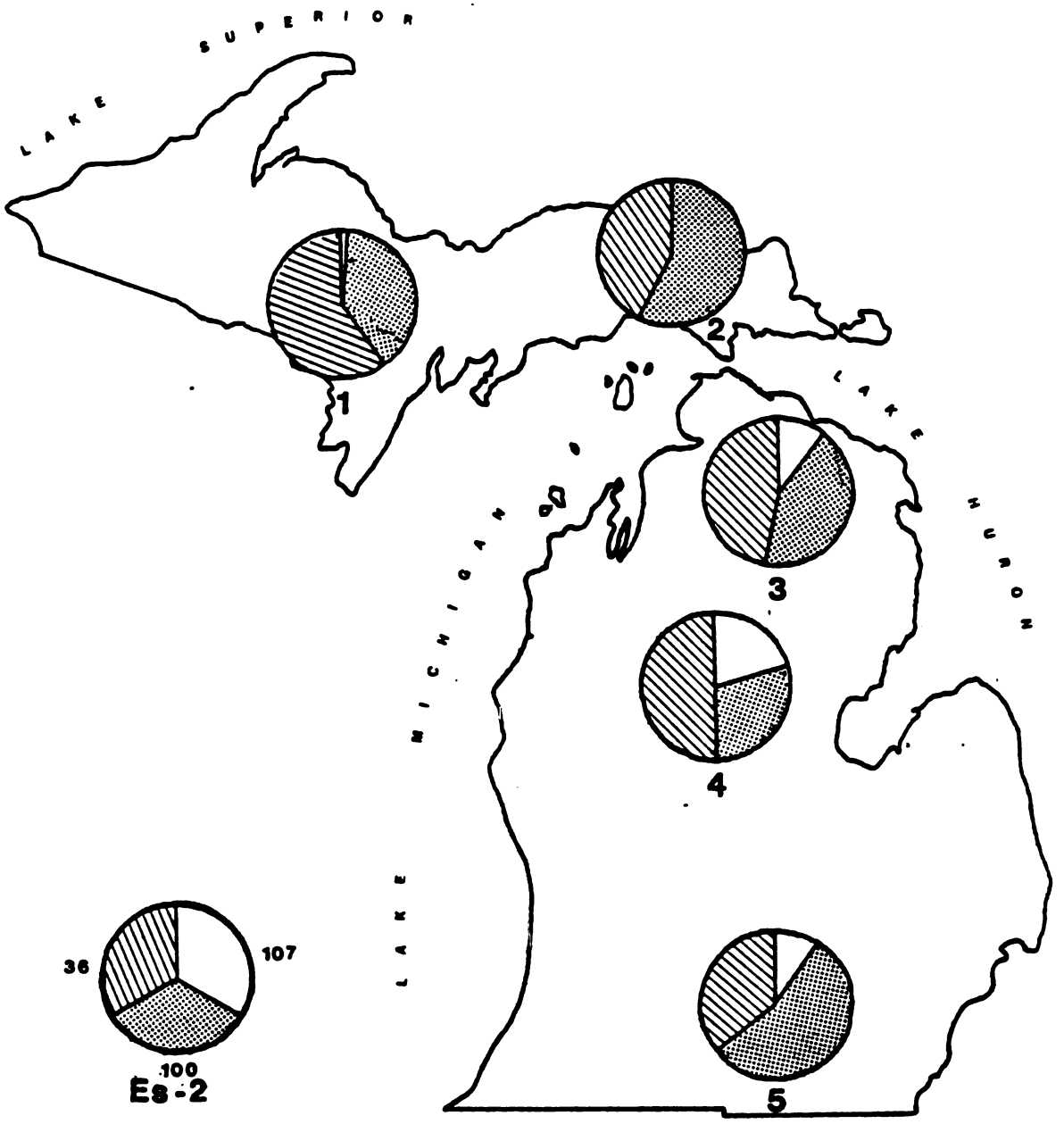



Figure 2. The distribution of three alleles for the Esterase-2 locus observed among deer in Michigan. Frequencies are expressed as proportions of a circle for each area.

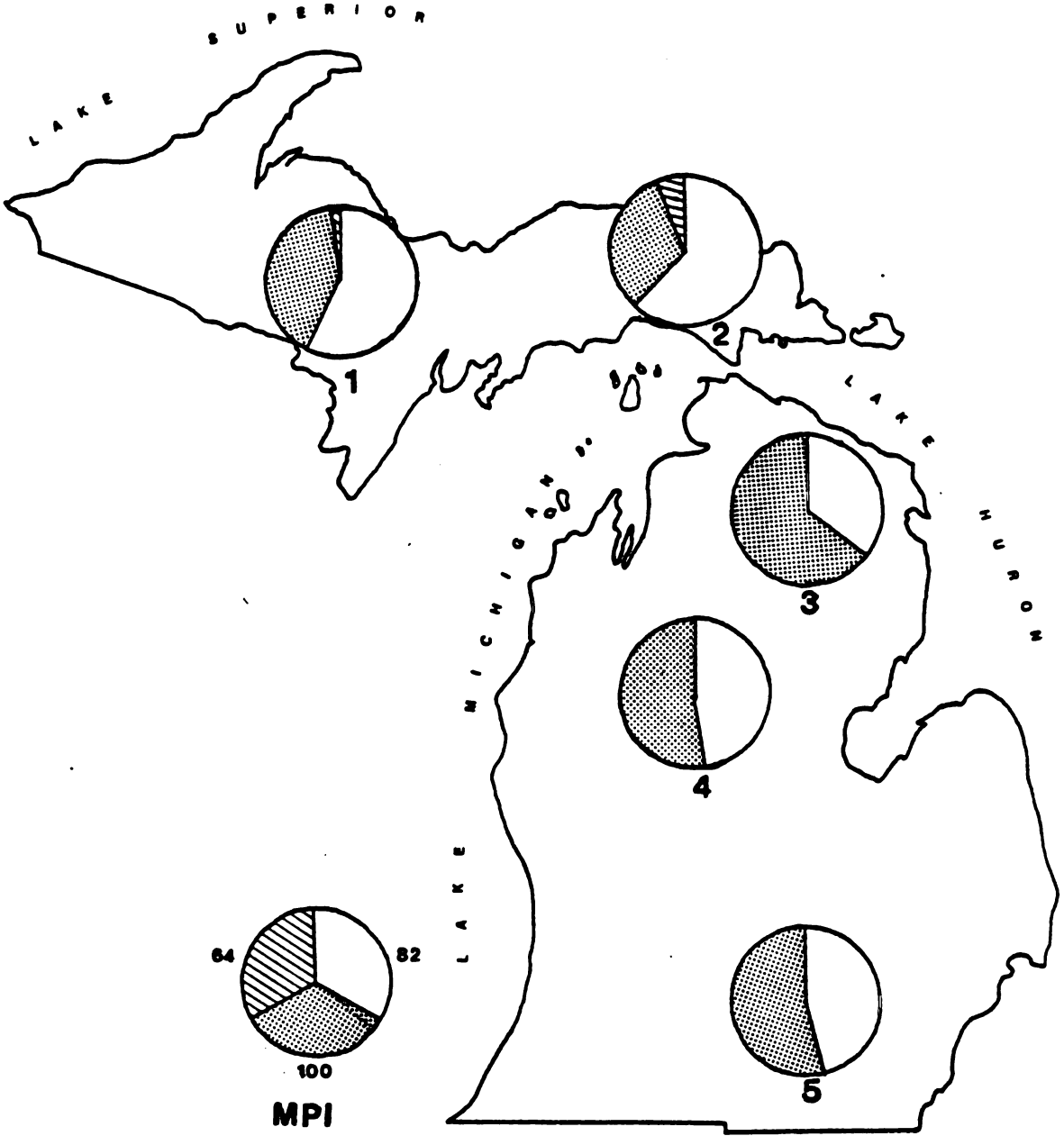



Figure 3. The distribution of three alleles for the MPI locus observed among deer in Michigan. Frequencies are expressed as proportions of a circle for each area.

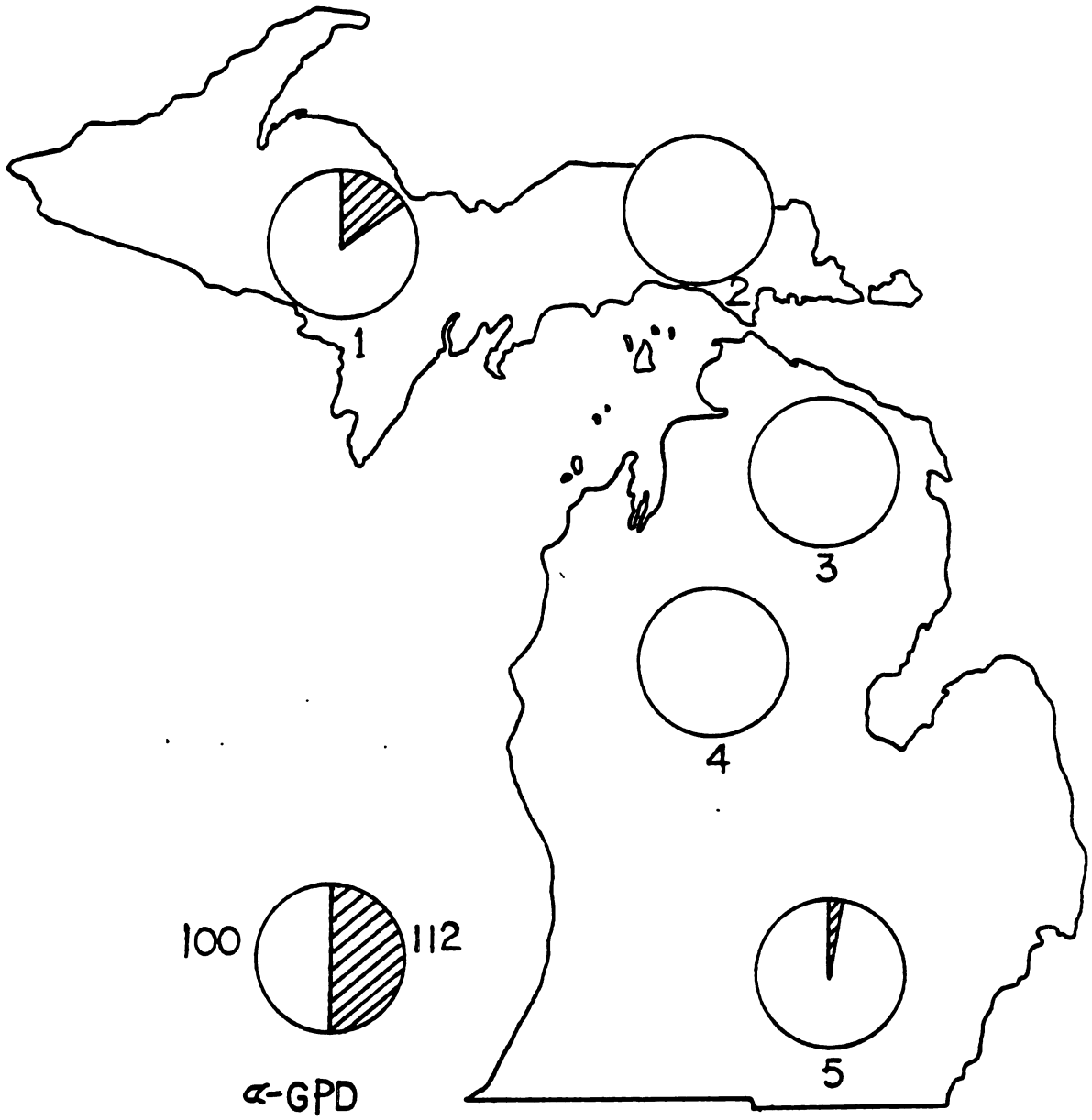



Figure 4. The distribution of two alleles for the GPD locus observed among deer in Michigan. Frequencies are expressed as proportions of a circle for each area.

The highest values are associated with combinations having the most discrepant gene frequencies between areas. The lowest mean $F_{ST}$ is observed among Lower Peninsula populations, reflecting a more homogenous genetic structure across these populations than between the Upper and Lower Peninsulas or the eastern and western Upper Peninsulas. These means are within the range of $F_{ST}$ values observed for inter-population comparisons within a much more restricted area (300 sq. mi.) in South Carolina (Manlove, 1977; R. Chesser, unpublished data). This type of comparison is not particularly meaningful, however, without knowledge of the relative stability of gene frequencies through time. Some areas of the Savannah River Plant in South Carolina show marked changes in gene frequencies among deer from year to year; other areas less so. We would expect that the differences observed between "populations" sampled from a larger geographic area, particularly where they are mutually isolated as between the Upper and Lower Peninsulas, are considerably more stable in time.

Some perspective on the relationship of $F_{ST}$ estimates to population structure might be gained by comparing values for other species' populations. The mean $F_{ST}$ for house mice (Mus musculus) among barns within farms in Texas (Selander, 1970) was .0245, and was .1737 among farms. Colonies of brown snails (Helix aspersa) had an $F_{ST}$ of .0337 among colonies within city blocks, .1161 among sample sites within cities and .1620 among cities in California

TABLE 3. $F_{ST}$ values for nine polymorphic loci in deer, calculated across various sample-area combinations in Michigan.

| | AREAS | | | | |
|---|---|---|---|---|---|
| LOCUS | 1,2,3, 4 & 5 | 1 & 2 | 3,4&5 | 2 & 3 | 1 & 5 |
| ES-2 | .0261 | .0362 | .0137 | .0248 | .0526 |
| MPI | .0392 | .0090 | .0137 | .0861 | .0176 |
| 6-PGD | .0008 | .0166 | .0003 | .0052 | .0005 |
| ME-1 | .0155 | .0150 | .0061 | .0024 | .0250 |
| ME-2 | .0177 | .0219 | .0160 | .0226 | .0214 |
| MDH-1 | .0178 | .0034 | .0035 | .0026 | .0284 |
| GOT-2 | .0372 | .0400 | .0010 | .0623 | .0004 |
| PGM-2 | .0132 | .0008 | .0137 | .0060 | .0014 |
| α-GPD-2 | .0773 | .0552 | .0423 | 0 | .0191 |
| $\bar{X}$ | .0272 | .0220 | .0122 | .0236 | .0185 |

(Selander and Kaufman, 1975). Genetic subdivision among bluegill samples within man-made reservoirs is lower ($F_{ST}$=0.029) than among reservoirs within a common drainage system ($F_{ST}$=0.392; Avise and Felly, 1979). Some values reported for human populations are .0007 among prefectures on the Japanese mainland and .0019 among islands (Nei and Imaizumu, 1966), .0633 among villages of Yanomama Indians (Neel and Ward, 1972) and .148 among mainland populations worldwide. By these comparisons, genetic subdivision among deer from major geographic regions of Michigan is similar to that observed for house mice among barns, somewhat greater than among human settlements on the Japanese mainland, and less than among populations of bluegill between reservoirs sharing the same drainage.

A summation of genetic differences between the five Michigan populations is provided by deriving Nei's distance coefficient for each of ten possible pair-wise comparisons (Table 4). This index is most often applied to interspecific and higher taxonomic comparisons but may be legitimately applied to population comparisons although numerical differences are very small. Genetic distance between conspecific mainland populations of mammals is usually low ($D<.05$), and in this respect deer are no exception. Within time periods short enough to neglect mutation rates, D is an indicator of the degree of sexual isolation and/or differential selection between large, panmictic and otherwise completely isolated populations. Certainly none

TABLE 4. Distance coefficients (D; Nei, 1972), for pair-wise comparisons of deer from five areas in Michigan.

| | 2 | 3 | 4 | 5 |
|---|---|---|---|---|
| 1 | .0081 | .0052 | .0038 | .0050 |
| 2 | | .0080 | .0057 | .0049 |
| 3 | | | .0017 | .0020 |
| 4 | | | | .0024 |

of the deer populations in any areas compared here is devoid of gene flow from and into other adjacent areas, and the amount of panmixia could vary considerably between them.

Comparisons of the three Lower Peninsula populations yield consistently lower D values than any comparison involving either of the two Upper Peninsula areas. The genetic distance between areas 2 and 3 across the Mackinaw Strait is greater than expected from the relative differences apparent between the three Lower Peninsula populations which are of comparable geographic distance from each other. This conforms to the results of a previous morphological study of Michigan deer by Rees (1970). Using a discriminate function analysis of variation in 10 cranial and 14 mandibular measurements, he found a significantly greater difference in his first canonical variate (characterized by an inverse relationship of zygoma and foramen magnum widths), between the Upper Peninsula and the northern and southern Lower Peninsulas than between contiguous Upper or Lower Peninsula populations. He ascribed this difference to the

effects of isolation since the post-glacial expansion of the Mackinaw Strait (approx. 9,500 yrs; Farrand and Eschman, 1974). His second canonical variate (characterized by an inverse relationship between cranial and palatal lengths) revealed relatively extreme differences between eastern and western Upper Peninsula deer compared to differences between the northern Lower Peninsula and the eastern or western Upper Peninsula. The electrophoretic data suggest that the genetic distance between eastern and western Upper Peninsula deer are as great as between deer on opposite banks of the strait. On the basis of both morphological and biochemical data, the ecological differences observed between the eastern and western areas of the Michigan Upper Peninsula are correlated with a degree of divergence comparable to that of populations directly isolated by the Mackinaw Strait.

These results should be recognized as reflecting differences in genetic structure among the populations at a single point in time. While the more obvious aspects of subdivision between Upper and Lower Peninsula deer represent the effects of geologically recent isolation, the apparent genetic homogeneity among Lower Peninsula populations may be deceiving. These populations could differ dramatically in the relative stability through time of gene frequencies they maintain. The effects of selection or stochastic processes upon them cannot be discerned at this time, and the rate of gene flow by effective dispersal of deer across

any given distance is not known.

## RECOMMENDATIONS

Future research using genetic indices along with other parameters to study deer populations in Michigan can take two major directions. On a large geographic scale, genetic comparisons should be extended to include other areas in the Upper Great Lakes region which have undergone varying rates of community evolution and habitat change since the Pleistocene. As a direct extension of the present study, knowing the genetic structure of several populations along the western shore of Lake Michigan would help determine the relative similarity of these populations to Upper Peninsula and southern Lower Peninsula deer. Similar comparisons of other mammal species with differing dispersal rates and known times of colonization and existence in a given area would be especially interesting and useful for comparing post-glacial evolutionary rates.

At the population level, much remains to be done to gain predictability in what we learn of the relationship of genetic structure to demographic processes. If island populations in the Great Lakes region have significantly reduced levels of variability, for example, we should study these populations to see if their demography is consequently different when compared to nearby mainland populations of the same genetic source. Also, the genetic effects of intense management practices as conducted in such areas as

the George Reserve in Livingston County and the enclosed herd at Cusino in Alger County are completely unknown. In these circumstances, where experimental manipulation of densities and age and sex specific mortality can be conducted under controlled conditions, exists the greatest potential for progressive research on deer population genetics. Research on population genetics has, for a variety of practical reasons, predominately involved studies of small mammals and a few other commonly studied vertebrate and invertebrate species with relatively high fecundity and short generation time. The application of theories developed from this work to deer biology requires, however, that descriptive and experimental work be done with deer. Given the importance of the species as an economic and recreational resource and the value of applying optimal management practices under a variety of ecological conditions, the genetic processes of deer populations responding to and confronting such practices cannot realistically be ignored.

## LITERATURE CITED


Avise, J. C., M. H. Smith, R. K. Selander, T. E. Lawlor and P. R. Ramsey. 1974. Biochemical polymorphism and systematics in the genus Peromyscus. V. Insular and mainland species of the subgenus Haplomylomys. Syst. Zool. 23:226-238.

Avise, J. C. 1976. Genetic differentiation during speciation. Pp. 106-122 in F. J. Ayala (ed.) Molecular Evolution. Sinauer Assoc. Inc., Sunderland, Mass.

Avise, J. C. and J. Felley. 1979. Population structure of freshwater fishes I. Genetic variation of bluegill (Lepomis macrochirus) populations in man-made reservoirs. Evol. 33:15-26.

Baccus, R., N. Ryman, M. H. Smith, C. Reuterwall and D. Cameron. Genetic variation and differentiation of large grazing species (Artiodactyls). Am. Soc. Mamm. Symp. Genet. In press.

Bonnell, M. L., and R. K. Selander. 1974. Elephant seals: Genetic variation and near extinction. Science 184:908-909.

Cavalli-Sforza, L. L. 1966. Population structure in human evolution. Proc. Roy. Soc., Ser. B 164:362-379.

Farrand, W. R., and D. F. Eschman. 1974. Glaciation of the Southern Peninsula of Michigan: a review. Mich. Academ. 7:31-56.

Harris, H., and D. A. Hopkinson. 1972. Average heterozygosity per locus in man: an estimate based on the incidence of enzyme polymorphism. Ann. Hum. Genet. 36:9-20.

Harris, J. 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.

Johns, P. E., R. Baccus, M. N. Manlove, J. E. Pinder, III, and M. H. Smith. Reproductive patterns, productivity and genetic variability in adjacent white-tailed deer populations. Proc. S. E. Assoc. Game & Fish Comm. 31:in press.

King, M., and A. C. Wilson. 1975. Evolution at two levels in humans and chimpanzees. Science 188:107-116.

Kristjansson, R. K. 1963. Genetic control of two pre-albumins in pigs. Genetics 48:1059-1063.

Manlove, M. N., J. C. Avise, H. O. Hillestad, P. R. Ramsey, M. H. Smith and D. O. Straney. 1976. Starch-gel electrophoresis for the study of population genetics in white-tailed deer. Proc. S. E. Assoc. Game and Fish Comm. 29:394-403.

Manlove, M. N., M. H. Smith, H. O. Hillestad, S. E. Fuller, P. E. Johns and D. O. Straney. 1977. Genetic subdivision in a herd of white-tailed deer as demonstrated by spatial shifts in gene frequencies. Proc. S. E. Assoc. Game and Fish Comm. 30:487-492.

Manlove, M. N., R. Baccus, M. R. Pelton, M. H. Smith, and D. Graber. Biochemical variation in the black bear (Ursus americanus). Proc. 3rd Ann. Internat. Symp. Bear Biology. In press.

Neel, J. V., and R. H. Ward. 1972. The genetic structure of a tribal population, the Yanomama Indians. VI. Analysis by F statistics. Genetics 72:639-666.

Nei, M. 1972. Genetic distance between populations. Am. Natur. 106:283-292.

Nei, M., and Y. Imaizumi. 1966. Genetic structure of human populations. I. Local differentiation of blood group gene frequencies in Japan. Heredity 21:9-35.

Ramsey, P. R., J. C. Avise, M. H. Smith and D. F. Urbston. 1979. Biochemical variation and genetic heterogeneity in South Carolina deer populations. J. Wildl. Manage. 43:136-142.

Rees, J. W. 1970. A multivariate morphometric analysis of divergence in skull morphology among geographically contiguous and isolated groups of white-tailed deer (Odocoileus virginianus) in Michigan. Evol. 24:220-229.

Selander, R. K. 1970. Behavior and genetic variation in natural populations. Amer. Zool. 10:53-66.

Selander, R. K., 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). Stud. in Genet., VI, Univ. Texas Publ. 7103:49-90.

Selander, R. K., and D. W. Kaufman. 1975. Genetic structure of populations of the brown snail (Helix aspersa). I. Microgeographic variation. Evol. 29:385-401.

Smith, M. H., C. T. Garten, and P. R. Ramsey. 1975. Genic heterozygosity and population dynamics in small mammals. Pp. 85-102 in C. L. Markert (ed.) Isozymes IV; Genetics and evolution. Academic Press, New York.

Smith, M. H., H. O. Hillestad, M. N. Manlove and R. L. Marchinton. 1976. Use of population genetics data for the management of fish and wildlife populations. Trans. 41st N. Am. Wildl. Nat. Resour. Conf.

Smith, M. H., M. N. Manlove and J. Joule. 1978. Spatial and temporal dynamics of the genetic organization of small mammal populations. In D. Snyder (ed.) Populations of Small Mammals under Natural Conditions. Univ. Pittsburgh Press. 5:99-113.

Smith, M. H., R. Baccus, H. O. Hillestad and M. N. Manlove. Population genetics of the white-tailed deer. In L. Halls (ed.). Ecology and Management of White-tailed deer. Stackpole Publ. Co., New York. In press.

Zimmerman, E. G., C. W. Kilpatrick and B. J. Hart. 1978. The genetics of speciation in the rodent genus Peromyscus. Evol. 32:565-579.