GENETIC VARIATION AND POPULATION DIFFERENTIATION IN WHITE-TAILED DEER (*ODOCOILEUS VIRGINIANUS*) REVEALED BY PCR-SSCP OF THE MAJOR HISTOCOMPATIBILITY COMPLEX

By

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CHAPTER I

ABSTRACT

Natural populations are exposed continually to environmental forces and anthropogenic perturbations that may alter their genetic structure and therefore their evolutionary fate. Because MHC class I and II gene products are an important part of the first line of defense in an immune response against foreign pathogens, it has been suggested that MHC differentiation among populations may be a direct reflection of the differing habitats and associated pathogens to which they are exposed. Unfortunately, the role that environmental and human-induced perturbations play in evolution and maintenance of variability at MHC loci, and the levels of MHC variability in natural populations, is poorly understood. To provide baseline data on levels of MHC genetic variation within and among seven populations of white-tailed deer, exon 2 of the class II *Mhc-DRB* locus was examined via Single-Strand Conformation Polymorphism (SSCP) analysis. This study has documented that although white-tailed deer were virtually extirpated from the eastern United States, high levels of genetic variability remain at the *Mhc-DRB* locus. If MHC allelic diversity is important for defense against pathogens, white-tailed deer may have survived this bottleneck with sufficient MHC allelic diversity to combat pathogenic invasions. Additionally, although white-tailed deer have been transplanted throughout this region, significant genetic differentiation over macro- and micro-geographic scales provides support for the hypothesis that MHC differentiation is a direct reflection of differing pathogenic environments.

CHAPTER II

INTRODUCTION

Natural populations are exposed continually to environmental forces that may alter their genetic structure and therefore, their evolutionary fate. Although most species have evolved intrinsic mechanisms to cope with fluctuations in spatial, temporal, density-dependent, and environmental variables, many natural populations must now also cope with anthropogenic perturbations such as habitat fragmentation and reduction, overexploitation, pollution, and transgeographic reintroduction (Leberg et al., 1994; Scribner, 1993). Such human-induced factors may result in local extinction, reduced gene flow, lowered effective population size, loss of genetic variability, increased inbreeding, and the inability to cope with future environmental perturbations (Lande, 1988; Leberg et al., 1994; Scribner, 1993). Because large mammals typically are long-lived, have long generation times, and have comparatively low habitat specificity, they may be particularly susceptible to anthropogenic changes in their environments (Scribner, 1993). Correlation between environmental or human-induced perturbations and allozymic variation has been documented (Chesser et al., 1982; Leberg et al., 1994; Scribner, 1993; Scribner and Chesser, 1993; Scribner et al., 1991), which suggests that such stressors could influence genetic loci that are adaptively significant and directly affect fitness.

The Major Histocompatibility Complex (MHC) is central to dictating the nature of immune responsiveness and contains some of the most polymorphic functional loci in vertebrates (Kaufman et al., 1990; Klein, 1986; Trowsdale, 1995; Wakeland et al., 1990). Because MHC class I and II gene products are the first line of defense in immune response against foreign pathogens, it has been suggested that MHC differentiation among populations may be a direct reflection of the differing habitats and associated pathogens to which they are exposed (Hedrick, 1996; Klein and Figueroa, 1981; Murray

et al., 1995; Slade, 1992; Wettstein et al., 1996). For these reasons, plus the correlation between variation at MHC loci and fitness indices, susceptibility to infectious diseases, and parasites (Apanius et al., 1997; Crew, 1993; Finch, 1990; Finch and Rose, 1995; Paterson et al., 1998; von Schantz et al., 1996), it has been suggested that variation at MHC loci should be especially important for evaluating survival capabilities of populations under times of stress (Wettstein and States, 1986*a*), and also should be considered a component of the design of management and conservation programs (Edwards and Potts, 1996; Hedrick and Parker, 1998; Hughes, 1991).

Unfortunately, the role that environmental and human-induced perturbations play in the evolution and maintenance of variability at MHC loci, as well as the levels of MHC variability in natural populations, is poorly understood (Wettstein et al., 1990). Therefore, the purpose of this study was to provide baseline data on levels of MHC variability within and among geographically disjunct populations of white-tailed deer (*Odocoileus virginianus*). White-tailed deer are an excellent model organism for evaluating effects of environmental and human-induced perturbations on levels of MHC genetic variability in natural populations for several reasons. First, white-tailed deer are geographically widely distributed (Hiller, 1996; Rue, 1978), and therefore, populations are exposed to a variety of environmental factors (temperature, precipitation, and pathogens) that should be reflected in genetic composition of MHC loci among populations (Klein and Figueroa, 1981; Murray et al., 1995; Slade, 1992; Wettstein et al., 1996). Second, MHC genetic variation within and among populations of red deer (*Cervus elaphus*; Swarbrick et al., 1995), moose (*Alces alces*; Mikko and Andersson, 1995), and African buffalo (*Syncerus caffer*; Wenink et al., 1998) provide a comparative background for interpretation of results from this study on white-tailed deer. Mikko and Andersson (1995) detected unusually low levels of *Mhc-DRB* variation within and among North American and European populations of moose. This low level of MHC variation has been attributed to either a historical population bottleneck (Mikko and Andersson,

1995) or reduced parasite exposure due to the solitary existence of moose (Ellegren et al., 1996; Hedrick and Gilpin, 1996). Supporting the hypothesis that reduced parasitic infection is responsible for low MHC variability in moose is documentation of high *Mhc-DRB* variation in African buffalo populations. Wenink et al. (1998) concluded that, although African buffalo probably endured a population bottleneck in the past, genetic variation at the *Mhc-DRB* locus was maintained due to herd structure and the need for African buffalo to maintain high levels of MHC variation in order to combat a diverse parasitic fauna.

Similar to moose and African buffalo, during settlement of the eastern United States, white-tailed deer populations were either extirpated or reduced to low numbers (Leberg et al., 1994; Sheffield et al., 1985), thereby reducing within-population variation and increasing among-population differentiation due to geographic isolation and genetic drift. Because of historical similarities among African buffalo, moose, and white-tailed deer, an examination of levels of *Mhc-DRB* variation within white-tailed deer populations may provide insight into demographic (solitary versus herd structure) effects on the maintenance and evolution of MHC variability. Additionally, examination of within- and among-population levels of *Mhc-DRB* variation may provide insight into other anthropogenic factors affecting white-tailed deer. For example, white-tailed deer should show an effect of isolation by distance (Wright, 1969), with those populations in closer geographic proximity exhibiting less genetic differentiation than those populations separated by greater geographic distances. Through transgeographic reintroduction programs coupled with protective legislation and public awareness, white-tailed deer were restored to viable numbers throughout most of their historic range (Leberg et al., 1994; Sheffield et al., 1985). If reintroduction has played a significant role in the current genetic composition of white-tailed deer populations, it would be expected that relatedness of populations would be more reflective of reintroduction history than environmental factors associated with geographic proximity.

To provide baseline data on levels of MHC genetic variation within and among populations of white-tailed deer, exon 2 of the class II *Mhc-DRB* locus was examined via Single-Strand Conformation Polymorphism (SSCP) analysis (Orita et al., 1989*a*, 1989*b*). This locus was chosen because it encodes the functionally critical antigen-binding site (Brown et al., 1988), has been shown to be highly variable in a single population of white-tailed deer (Van Den Bussche et al., 1999), and will provide data comparable with population genetic studies of other artiodactyls (Mikko and Andersson, 1995; Swarbrick et al., 1995; Wenink et al., 1998).

CHAPTER III

MATERIALS AND METHODS

Tissue samples of 254 hunter-harvested white-tailed deer were collected from the following seven locations: McAlester Army Ammunition Plant, Pittsburg Co., Oklahoma (MAAP—n = 127); Dallas Co., Iowa (DC—n = 11); Hatchie National Wildlife Refuge, Haywood Co., Tennessee (HaNWR—n = 30); Chuck Swan Wildlife Management Area, Campbell and Union Cos., Tennessee (CSWMA—n = 21); Cheatham National Wildlife Refuge, Cheatham Co., Tennessee (CNWR—n = 19); Naples Biological Reserve in Southern New York (NBR—n = 20); and Huntington National Wildlife Refuge in Northern New York (HuNWR—n = 26); (Fig. 1).

Genomic DNA was isolated from frozen liver or muscle tissue following the protocol of Longmire et al. (1997). Amplification of the second exon of *Mhc-DRB* was accomplished via the Polymerase Chain Reaction (PCR; Saiki et al., 1988) using primers LA31, 5'-GATGGATCCTCTCTCTGCAGCACATTTCCT-3', and LA32, 5'-CTTGAATTCGCGTCACCTCGCCGCTG-3' (Mikko and Andersson, 1995; Sigurdardottir et al., 1991). These primers flank the functionally critical antigen-binding site and produce a product 390 base pairs in length. PCR was carried out using approximately 400 ng DNA in a final reaction volume of 50 µl consisting of 1 unit of *Taq* DNA polymerase (Promega; Madison, Wisconsin), 0.5 µM of each primer, 0.07 mM deoxynucleotides, and 2.0 mM $MgCl_2$. The thermal profile consisted of 95°C for 60 s, 50°C for 30 s, and 72°C for 60 s, followed by 72°C for 30 min and was conducted using a Perkin Elmer GeneAmp PCR System 9600.

Following amplification, all individuals were genotyped via SSCP (Orita et al., 1989*a*, 1989*b*). PCR amplicons were denatured by heating and immediately placed into ice water, loaded onto 5% nondenaturing acrylamide gels (acrylamide: bisacrylamide = 49:1) containing 10% glycerol, and subjected to electrophoresis at 300 Volts for 24 h

with a fan blowing on the gel. Following electrophoresis, acrylamide gels were transferred to Whatman paper, dried, and exposed to autoradiographic film.

To aid in genotyping individuals across gels, the 15 unique white-tailed deer alleles (*Odvi-DRB*01-15*) detected by Van Den Bussche et al. (1999) were run on every gel. Unique conformations not previously identified as one of the 15 alleles identified from white-tailed deer (Van Den Bussche et al., 1999) were cloned using the pGEM-T cloning system (Promega) for subsequent sequence analysis. For each cloned allele, SSCP was performed on PCR products of several recombinant clones using reaction conditions and thermal profile described previously. PCR amplicons from cloned inserts were run on acrylamide gels alongside amplified products from the individual these products were cloned. This approach allowed verification of recombinant clones that contained the correct allele with no PCR induced error. Amplicons of each unique allele were cleaned using the Wizard PCR Prep DNA Purification System (Promega) and sequenced in both directions using a Perkin-Elmer Applied Biosystems 377 automated sequencer.

To examine the phylogenetic affinities of new *Mhc-DRB* alleles detected in this study, a neighbor-joining phylogenetic tree (Saitou and Nei, 1987) was constructed utilizing the 62 cervid *DRB* alleles and 4 bovid *DQB* alleles examined by Van Den Bussche et al. (1999). The resulting neighbor-joining tree was based on corrected distance values (Kimura, 1980) under the minimum evolution criterion (Nei, 1991; Saitou, 1991). Following the recommendation of Swofford et al. (1996), the single neighbor-joining tree was used as the starting tree for a more thorough search using tree bisection-reconstruction (TBR) branch swapping and minimum evolution options in PAUP*4.02b (Swofford, 1999). Nomenclature of white-tailed deer *Mhc-DRB* alleles follows Klein et al. (1990) and Van Den Bussche et al. (1999). Following the identification and verification of a unique allele, this allele was run on all subsequent SSCP gels.

Allele frequencies were calculated for the observed data and analyses of gene diversity (H_e), equivalent to expected heterozygosity (Nei, 1987); deviation from Hardy-Weinberg expectations, using a procedure described in Guo and Thompson (1992); population differentiation using F-statistics (Nei, 1977, 1978; Wright, 1951) and analysis of molecular variance (AMOVA; Excoffier et al., 1992) were carried out using Arlequin version 1.1 (Schneider et al., 1997). POPGENE version 1.21 (Yeh et al., 1997) was used to calculate expected and observed heterozygosity and homozygosity, Nei's (1978) genetic distance (D), and a UPGMA dendrogram based on Nei's (1978) genetic distance. Finally, GENEPOP version 3.1c (Raymond and Rousset, 1995) was used to test for isolation by distance.

CHAPTER IV

RESULTS

Eighteen alleles were detected among these 254 individuals, including three new alleles (*Odvi-DRB*16, Odvi-DRB*17, Odvi-DRB*18*) that represent additional variants of the two major *Odvi-DRB* allelic lineages detected by Van Den Bussche et al. (1999; Fig. 2).

The number of *Odvi-DRB* alleles detected in the different populations under study ranged from 8 to 14 with a mean of 11.6 alleles per population (Table 1). Three alleles (*Odvi-DRB*07, Odvi-DRB*08*, and *Odvi-DRB*14)* were found in all seven localities, whereas *Odvi-DRB*13* and *Odvi-DRB*18* were unique to the MAAP and HuNWR populations of white-tailed deer, respectively. Together, both major *Odvi-DRB* lineages (Fig. 2) are found in each of the seven populations of white-tailed deer although distribution and frequency of these alleles vary among populations (Table 1). Within population gene diversity (H_e; Table 2) ranged from 0.674 to 0.915 revealing a high level of gene diversity within all populations, and all populations exhibited significant deviations from Hardy-Weinberg expectations. Comparison of observed (H_o) and expected (H_e) heterozygosity per population reveals that, with the exception of the MAAP population from southeastern Oklahoma, all populations exhibit a deficiency of heterozygotes. As would be expected, the fractional reduction of heterozygotes (F) is positive for all except the MAAP population in which a greater number of heterozygotes were observed than expected based on allele frequencies. The largest deviation from

expectation is observed at the CSWMA population, where 57% of the individuals examined were homozygous (Table 2).

Allelic frequency differences among populations were examined with measures of genetic distance (D; Nei, 1978) and genetic divergence (F_{ST}, Nei, 1978). Pairwise genetic distances ranged from 0.299 for the comparison of MAAP and HuNWR populations, to 2.194 between HuNWR and CNWR populations with a mean pairwise distance of 0.886 (Table 3). Pairwise values of F_{ST} weight the differences by within-population heterozygosity. Therefore, although all pairwise F_{ST} comparisons are high and most are statistically significant (Table 3), the lowest difference (which is not statistically different from 0) is between the DC and NBR populations because these two populations have the highest within-population heterozygosities (Table 2). Conversely, the largest pairwise F_{ST}-value is between HaNWR and HuNWR, the populations with the lowest gene diversity (Table 2). Significant genetic differentiation among populations was detected using AMOVA, (mean $F_{ST} = 0.1147$) indicating that 11.47% of the total variation was partitioned among populations with the remaining 88.53% found within populations (Table 4).

A UPGMA dendrogram constructed from Nei's D values, was constructed to depict the spatial pattern of allelic differences among populations (Fig. 3--Nei, 1978). Two clades were detected. However, clustering of populations does not agree with the geographic proximity of populations. For example, the geographically proximal populations (HuNWR and NBR) from southern and northern New York do not cluster together in that HuNWR is most similar to the DC population from Iowa and the NBR population is most similar to the CNWR population from central Tennessee.

Additionally, although the three populations sampled from Tennessee cluster together, the branching sequence does not follow geographic proximity (Figs. 1 and 3). An independent test of isolation by distance provides additional support for the lack of correlation between genetic distance and geographic distance (Fig. 4). Together, these results indicate something other than geographic proximity is probably responsible for clustering of populations (Fig. 3).

CHAPTER V

DISCUSSION

White-tailed deer are possibly one of North America's most intensively studied wild species, yet little is known about the genetic structure and relatedness of white-tailed deer populations throughout the distribution of the species. This study is the first attempt to elucidate geographic patterns of genetic variability for any MHC locus in white-tailed deer, therefore direct comparisons of these results to other genetic studies of the white-tailed deer MHC are not possible. However, within- and among-population patterns of *Odvi-DRB* variation will be compared to patterns of allozymic variation in white-tailed deer and *Mhc-DRB* variation in other artiodactyls.

Identification of 18 *Odvi-DRB* alleles among 254 white-tailed deer sampled from seven localities is similar to the number of *Mhc-DRB* alleles detected among four populations of African buffalo (Wenink et al., 1998). Both white-tailed deer and African buffalo survived severe population bottlenecks in the past, which may have resulted in a decreased number of alleles detected in these taxa relative to the 34 *Mhc-DRB* alleles detected in red deer (Swarbrick et al., 1995). Only 10 *Mhc-DRB* alleles were found in natural populations of North American and European moose (*Alces alces*--Mikko and Andersson, 1995). It has been suggested that this uncharacteristically low number of alleles may be due either to an ancient bottleneck (Mikko and Andersson, 1995) or be a result of the solitary lifestyle of moose. Among non-domesticated artiodactyls thus far examined (African buffalo, moose, red deer, and white-tailed deer), moose are the only taxon that exhibits a solitary lifestyle and possess low *Mhc-DRB* allelic diversity (Mikko

and Andersson, 1995; Van Den Bussche et al., 1999). Both white-tailed deer and African buffalo experienced population declines possibly equivalent to that experienced by moose, yet these two taxa have retained more *Mhc-DRB* allelic diversity. This indicates that lifestyle (solitary versus herd) may play a role in MHC allelic diversity. Pathogens infecting host populations comprised of solitary individuals are not easily spread throughout the population as in more gregarious hosts that often form large herds. Therefore, solitary individuals may require a lower level of *Mhc-DRB* allelic diversity to combat the spread of pathogens than individuals occurring in herds. This is one of the propositions to explain why MHC allelic diversity is so high in some populations and is also the basic premise behind the genetic herd-immunity model for the maintenance of MHC polymorphism (Wills and Green, 1995).

An additional factor to explain the maintenance of MHC polymorphism may relate to the environment in which each of these taxa occur (Trowsdale et al., 1989). Moose occur in cold, northern climates, whereas white-tailed deer cover a broad geographic region, extending from southern Canada through Central America to northern South America. Similarly, African buffalo inhabit a large geographic area extending throughout most of Africa. Consequently, taxa that are distributed over broad geographic areas are exposed to a greater variety of pathogens, which in turn may require a greater diversity of MHC allelic variants to effectively combat these pathogens.

Although allelic diversity is high within each population of white-tailed deer, within-population heterozygosity is low when compared to results from African buffalo (Wenink et al., 1998). Observed heterozygosity was highest in the MAAP and NBR populations and lowest in the HuNWR population (Table 2). The similar, albeit low,

heterozygosity observed in five of the seven populations was unexpected. During settlement, white-tailed deer were virtually extirpated from most areas east of the Mississippi River. However, restocking with individuals from other areas of North America resulted in most areas maintaining viable populations. Because most areas were restocked with white-tailed deer from numerous sources (Blackard, 1971; Hillestad, 1984; Kennedy et al., 1987; Leberg et al., 1994), it was anticipated that these seven populations would exhibit high heterozygosity, similar to African buffalo (Wenink et al., 1998).

Although the population of white-tailed deer from MAAP had the highest heterozygosity ($H_o = 0.811$) and the largest sample size ($n = 127$), it is unlikely that reduced heterozygosity in other populations was simply due to stochastic sampling error. White-tailed deer from northern New York (HuNWR) exhibited the lowest observed heterozygosity ($H_o = 0.320$), yet more than twice as many individuals were sampled from this population than were sampled from Iowa (DC) for which the observed heterozygosity was 1.4-times greater (Table 2). A second possibility is that lower heterozygosity in these populations is due to the presence of null alleles. The failure of primers to amplify alleles from other *Odvi-DRB* allelic lineages would result in decreased heterozygosity and suggest that at present, only a small fraction of the *Odvi-DRB* alleles have been identified. Alternatively, results reported herein may be real and the low levels of heterozygosity may be reflective of inbreeding, differential management practices and hunting pressures, or different pathogenic environments. All of these factors could select for different *Odvi-DRB* alleles, and thus, affect genotypic ratios (Lochmiller, 1996; Wettstein and States, 1986*a*, 1986*b*; Wettstein et al., 1990, 1996). Continued study of MHC loci in white-

tailed deer should provide insight into levels and significance of heterozygosity within white-tailed deer populations.

The level of spatial genetic differentiation among populations of white-tailed deer (F_{ST} = 11.47%) is equivalent to that detected among distant populations of African buffalo (G_{ST} = 11.03%; Wenink et al., 1998) and may be indicative of isolation by distance. Previous genetic studies of white-tailed deer have produced conflicting results as to the documentation of isolation by distance. Gavin and May (1988) detected a significant correlation between genetic differentiation and geographic distance for comparison of deer from eastern and western United States. However, Ellsworth et al. (1994) and Leberg et al. (1994) failed to detect significant levels of isolation by distance for white-tailed deer in the southeastern United States. Leberg et al. (1994) concluded that transgeographic reintroduction of large numbers of individuals (≥ 25) to re-establish white-tailed deer throughout the southeastern United States prevented the pattern of isolation by distance that has been detected in many other populations of vertebrates. Kennedy et al. (1987) examined spatial patterns of allele frequencies within and among 29 populations of white-tailed deer from Tennessee and identified association based on geographic proximity and stocking history. However, the hierarchical analysis indicated that physiogeographic region accounted for more of the total gene diversity than herd origin. These results led Kennedy et al. (1987) to conclude that herd origin, gene flow, and selection appear to be involved in shaping the genetic diversity of white-tailed deer in Tennessee.

Examination of pairwise F_{ST}-values (Table 3) revealed that overall genetic differentiation probably cannot be explained simply with isolation by distance. White-

tailed deer were examined from two localities in New York (NBR and HuNWR) and three localities in Tennessee (CNWR, CSWMA, and HaNWR). Significant genetic differentiation was detected between the two New York populations and two of the three pairwise comparisons for Tennessee populations. Moreover, the pairwise F_{ST}-value between populations of white-tailed deer from Iowa (DC) and southern New York (NBR) did not differ significantly from zero (Table 3). Finally, no significant correlation was detected between genetic differentiation and geographic distance (Fig. 4).

Because genetic differentiation is weighted by heterozygosity and with the exception of the MAAP and NBR samples, a deficiency of heterozygotes was detected for all populations of white-tailed deer, a clustering analysis of populations based on Nei's (1978) genetic distance values was performed. Two main clusters were detected and, with the exception of the three Tennessee populations falling within one of the two main clusters, along with the population of white-tailed deer from southern New York, no clustering of geographically proximal populations was detected in this analysis. Although all populations have a relatively large number of *Odvi-DRB* alleles, one or two alleles are typically most frequent in each population, with the remaining alleles occurring at low frequency (Table 1). The clustering of DC, HuNWR, and MAAP populations of white-tailed deer from Iowa, northern New York, and southeastern Oklahoma, is most likely related to allele *Odvi-DRB*05*. Although this allele occurs in all but the CNWR population from Tennessee, it is the most frequent allele in the DC, HuNWR, and MAAP populations, with a frequency of 0.273, 0.560, and 0.323 respectively.

This study has documented high levels of genetic variability at the *Mhc-DRB* locus. If MHC allelic diversity is important for defense against pathogens (Apanius et al., 1997; Finch and Rose, 1995; Hedrick, 1996; Paterson et al., 1998), white-tailed deer may have survived this bottleneck with sufficient MHC allelic diversity to combat pathogenic invasions. Additionally, although white-tailed deer have been artificially moved throughout this region, significant genetic differentiation over macro- and micro-geographic scales provides support that MHC differentiation may be a direct reflection of their pathogenic environments (Klein and Figueroa, 1981; Murray et al., 1995; Slade, 1992; Wettstein et al., 1996). Although much attention has recently focused on the influence of environmental variables on MHC variation (Lochmiller, 1996), these studies have focused on animal populations that are either much more difficult to study (Murray et al., 1995; Slade, 1992) or for which the necessary information regarding population ecology, physiology, reproduction, and immunology are lacking (Wettstein and States, 1986*a*, 1986*b*; Wettstein et al., 1990, 1996). Because so much is known about the biology, physiology, nutrition, and reproduction of white-tailed deer, studies of MHC variability within and among populations of white-tailed deer will be of considerable interest in the future. Gaining a better understanding of these factors is not only useful to our understanding of MHC evolution, but examination of these factors in a species such as white-tailed deer could provide insight into the effectiveness of different management practices. For example, white-tailed deer are hunted throughout most of North America with the largest males receiving the strongest hunting pressure. If secondary sexual characteristics in white-tailed deer (antler size, width, and number of points, and body size and condition) are correlated with variation at MHC loci, as has been demonstrated

for ring-necked pheasants (von Schantz et al., 1996), then such hunting practices may be detrimental to the overall health of the population.

It recently has been proposed that variation at MHC loci is so critical to the health of populations that conservation and management practices should focus solely on maintaining variation at these loci (Hughes, 1991). White-tailed deer are an excellent organism to test this hypothesis. Because most state wildlife agencies maintain records on the health of deer populations via standard body indices, a valuable data set exists for evaluating the genotypes of individuals harvested and the individuals' reproductive and nutritional health. Management practices for white-tailed deer vary considerably across the species' distribution making it possible to evaluate the effect of management practice on MHC variability and overall health of populations. One such management practice that recently has received considerable attention, but for which its affect on MHC variability has not been examined, is reintroduction (Ellsworth et al., 1994; Hedrick and Parker, 1998; Kennedy et al., 1987; Leberg, 1990*a*, 1990*b*, 1991, 1993; Leberg and Ellsworth, 1999; Leberg et al., 1994; Scribner, 1993). This study has revealed levels of within-population variability and among-population differentiation at the *Mhc-DRB* locus that are sufficient to allow examination of the effect of management practices, environment, and anthropogenic perturbations on the genetic structure of *Mhc-DRB* variability in white-tailed deer. Finally, examination of other cervids could provide additional insight into MHC evolution, the significance of variation at these loci, and the role of environmental and anthropogenic factors on maintaining variation at these loci.

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Table 1.--Occurrence and frequency of *Odvi-DRB* alleles in seven populations of white-tailed deer. Populations are as follows: MAAP, McAlester Army Ammunition Plant; DC, Dallas County; HaNWR, Hatchie National Wildlife Refuge; CNWR, Cheatham National Wildlife Refuge; CSWMA, Chuck Swan Wildlife Management Area; NBR, Naples Biological Reserve; HuNWR, Huntington National Wildlife Refuge. *n* = number of individuals sampled from each population.

	Population *(n)*						
Allele	MAAP (127)	DC (11)	HaNWR (30)	CNWR (18)	CSWMA (21)	NBR (21)	HuNWR (25)
*Odvi-DRB*01*	0.024	-------	0.017	0.222	0.095	0.048	-------
*Odvi-DRB*02*	-------	-------	0.050	0.056	-------	0.119	-------
*Odvi-DRB*03*	0.020	-------	0.033	-------	0.191	-------	-------
*Odvi-DRB*04*	0.272	-------	0.033	-------	-------	0.024	-------
*Odvi-DRB*05*	0.323	0.273	0.017	-------	0.048	0.048	0.560
*Odvi-DRB*06*	0.008	0.182	-------	0.028	0.048	0.119	-------
*Odvi-DRB*07*	0.142	0.046	0.050	0.306	0.095	0.143	0.020
*Odvi-DRB*08*	0.012	0.136	0.150	0.139	0.048	0.024	0.060
*Odvi-DRB*09*	0.008	-------	-------	0.028	0.024	0.048	0.080
*Odvi-DRB*10*	0.012	0.136	0.050	0.056	0.024	0.071	-------
*Odvi-DRB*11*	0.043	0.046	0.050	-------	0.048	0.024	0.040
*Odvi-DRB*12*	0.047	-------	0.017	-------	0.024	0.119	0.040
*Odvi-DRB*13*	0.008	-------	-------	-------	-------	-------	-------
*Odvi-DRB*14*	0.075	0.136	0.433	0.083	0.048	0.167	0.080
*Odvi-DRB*15*	0.008	-------	0.067	0.083	0.048	-------	0.040
*Odvi-DRB*16*	-------	-------	-------	-------	0.167	0.048	0.020
*Odvi-DRB*17*	-------	0.046	0.033	-------	0.095	-------	-------
*Odvi-DRB*18*	-------	-------	-------	-------	-------	-------	0.060

Table 2.—Number of *Odvi-DRB* alleles (A), sample size (n), expected heterozygosity (H_e), observed heterozygosity (H_o), and fractional reduction of heterozygosity (F) within seven populations of white-tailed deer. Populations are as follows: MAAP, McAlester Army Ammunition Plant; DC, Dallas County; HaNWR, Hatchie National Wildlife Refuge; CNWR, Cheatham National Wildlife Refuge; CSWMA, Chuck Swan Wildlife Management Area; NBR, Naples Biological Reserve; HuNWR, Huntington National Wildlife Refuge.

	Population						
	MAAP	DC	HaNWR	CNWR	CSWMA	NBR	HuNWR
A	15	8	13	9	14	13	10
n	127	11	30	18	21	21	25
H_e	0.794	0.870	0.784	0.840	0.915	0.915	0.674
	± 0.015	± 0.040	± 0.048	± 0.036	± 0.021	± 0.017	± 0.071
H_o	0.811	0.450	0.433	0.500	0.429	0.714	0.320
F*	-0.021	0.483	0.448	0.405	0.531	0.220	0.525

* $F = 1 - (H_o / H_e)$

Table 3.--Pairwise differences between seven populations of white-tailed deer using two measures of population differentiation. Nei's (1978) genetic distances (D) are above the diagonal and below the diagonal are pairwise F_{ST}-values. Statistically significant F_{ST}-values are denoted with an asterisk (*). Populations are as follows: MAAP, McAlester Army Ammunition Plant; DC, Dallas County; HaNWR, Hatchie National Wildlife Refuge; CNWR, Cheatham National Wildlife Refuge; CSWMA, Chuck Swan Wildlife Management Area; NBR, Naples Biological Reserve; HuNWR, Huntington National Wildlife Refuge.

	MAAP	DC	HuNWR	NBR	CNWR	CSWMA	HaNWR
MAAP	--------	0.462	0.299	0.778	1.179	1.179	1.262
DC	0.068*	--------	0.247	0.431	1.040	0.901	0.634
HuNWR	0.083*	0.071*	--------	1.182	2.194	1.373	1.522
NBR	0.092*	0.031	0.162*	--------	0.394	0.653	0.398
CNWR	0.136*	0.094*	0.226*	0.039	--------	0.634	0.810
CSWMA	0.113*	0.061*	0.170*	0.037	0.058	--------	1.040
HaNWR	0.159*	0.087*	0.223*	0.059*	0.112*	0.106*	--------

Table 4.--Analysis of Molecular Variance (AMOVA) test design and results.

Source of variation	d.f.	Sum of squares	Variance components	Percentage of variation
Among populations	6	21.037	0.0523	11.47
Within populations	499	201.429	0.4037	88.53
Total	505	222.466	0.4560	
Fixation index	$F_{ST} = 0.1147$			
$P \leq 0.0001$				

FIGURE LEGENDS

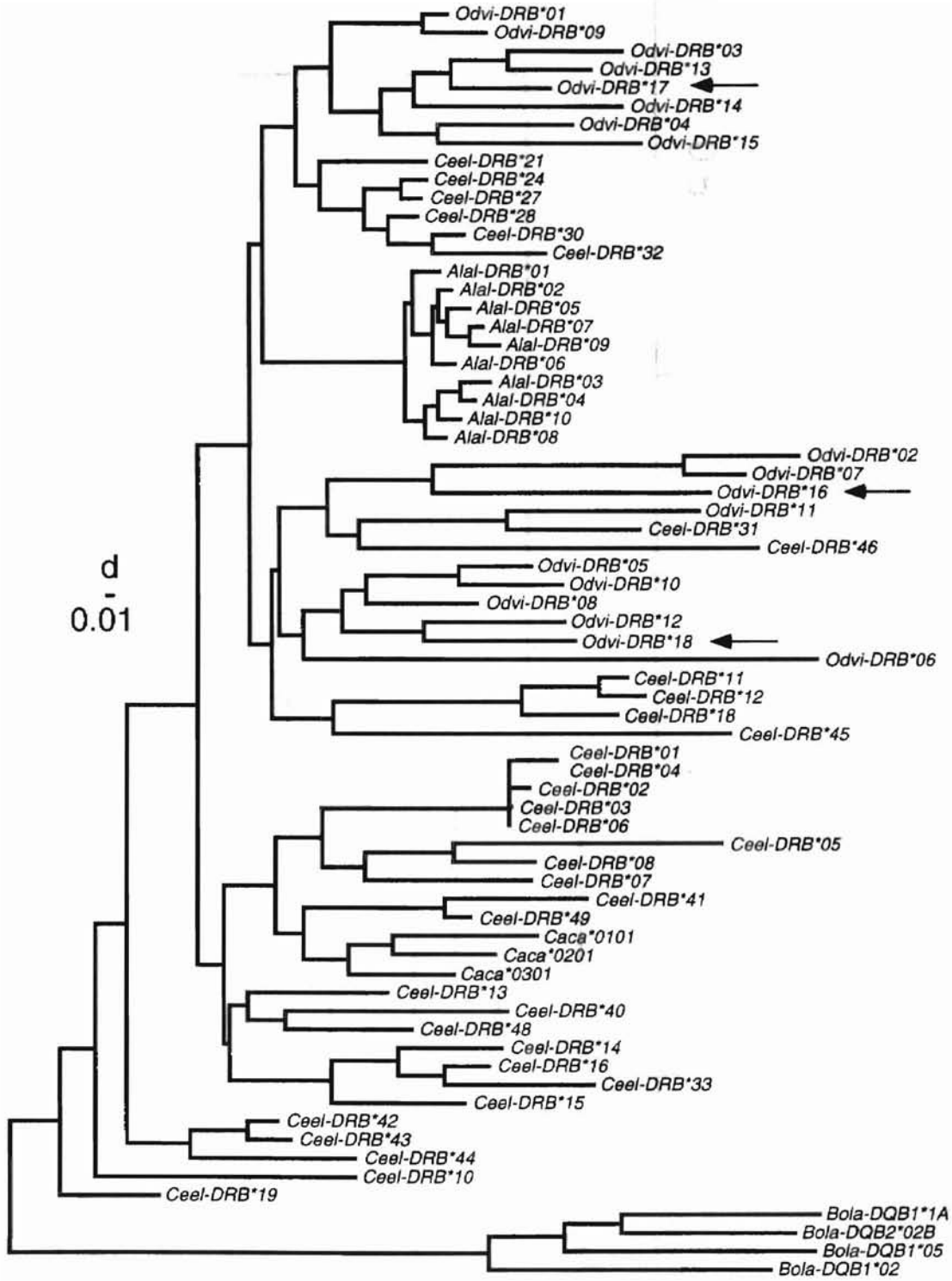
Fig. 1.--Locations of sampled white-tailed deer populations. Abbreviations are: MAAP, McAlester Army Ammunition Plant (n = 127); DC, Dallas County (n = 11); HaNWR, Hatchie National Wildlife Refuge (n = 30); CNWR, Cheatham National Wildlife Refuge (n = 18); CSWMA, Chuck Swan Wildlife Management Area (n = 21); NBR, Naples Biological Reserve (n = 21); HuNWR, Huntington National Wildlife Refuge (n = 25).

Fig. 2.--Neighbor-joining phylogenetic tree showing relationships of new *Odvi-DRB* alleles detected in this study (indicated with arrows) to previously published cervid *Mhc-DRB* and bovid *Mhc-DQB* alleles (Van Den Bussche et al., 1999). *Odvi* = white-tailed deer (*Odocoileus virginianus*), *Ceel* = red deer (*Cervus elaphus*), *Alal* = moose (*Alces alces*), and *Caca* = roe deer (*Capreolus capreolus*). The tree was rooted with cattle *Bola-DQB* sequences.

Fig. 3.--UPGMA dendrogram based on Nei's (1978) genetic distance values showing relationships among seven populations of white-tailed deer. Abbreviations are: MAAP, McAlester Army Ammunition Plant; DC, Dallas County; HaNWR, Hatchie National Wildlife Refuge; CNWR, Cheatham National Wildlife Refuge; CSWMA, Chuck Swan Wildlife Management Area; NBR, Naples Biological Reserve; HuNWR, Huntington National Wildlife Refuge.

Fig. 4.—Results of an isolation by distance analysis for seven populations of white-tailed deer.


HuNWR
NBR
DC
CSWMA
CNWR
HaNWR
MAAP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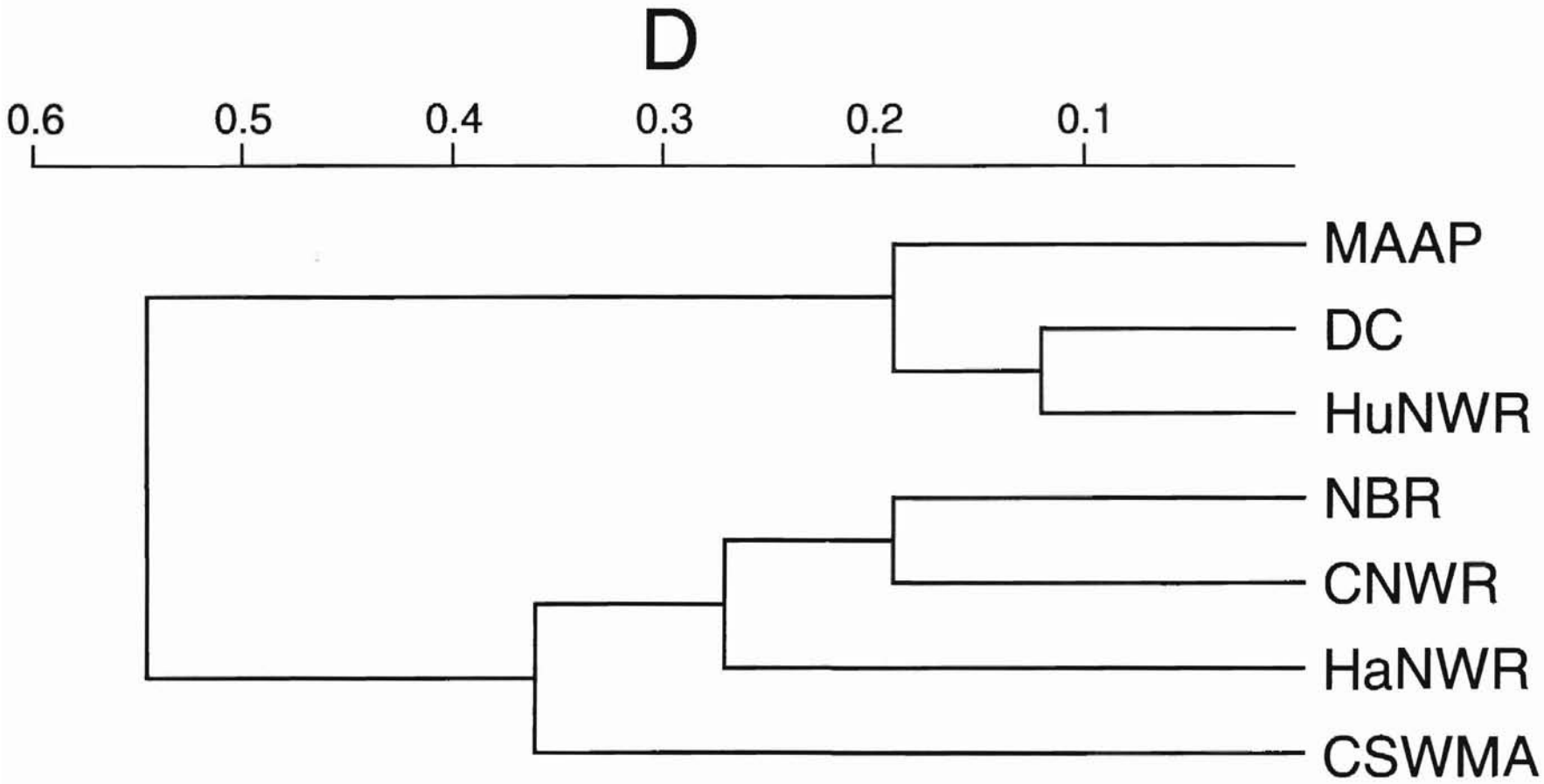
Odvi-DRB*09
Odvi-DRB*03
Odvi-DRB*13
Odvi-DRB*17
Odvi-DRB*14
Odvi-DRB*04
Odvi-DRB*15
Ceel-DRB*21
Ceel-DRB*24
Ceel-DRB*27
Ceel-DRB*28
Ceel-DRB*30
Ceel-DRB*32
Alal-DRB*01
Alal-DRB*02
Alal-DRB*05
Alal-DRB*07
Alal-DRB*09
Alal-DRB*06
Alal-DRB*03
Alal-DRB*04
Alal-DRB*10
Alal-DRB*08
Odvi-DRB*02
Odvi-DRB*07
Odvi-DRB*16
Odvi-DRB*11
Ceel-DRB*31
Ceel-DRB*46
d
0.01
Odvi-DRB*05
Odvi-DRB*10
Odvi-DRB*08
Odvi-DRB*12
Odvi-DRB*18
Odvi-DRB*06
Ceel-DRB*11
Ceel-DRB*12
Ceel-DRB*18
Ceel-DRB*45
Ceel-DRB*01
Ceel-DRB*04
Ceel-DRB*02
Ceel-DRB*03
Ceel-DRB*06
Ceel-DRB*05
Ceel-DRB*08
Ceel-DRB*07
Ceel-DRB*41
Ceel-DRB*49
Caca*0101
Caca*0201
Caca*0301
Ceel-DRB*13
Ceel-DRB*40
Ceel-DRB*48
Ceel-DRB*14
Ceel-DRB*16
Ceel-DRB*33
Ceel-DRB*15
Ceel-DRB*42
Ceel-DRB*43
Ceel-DRB*44
Ceel-DRB*10
Ceel-DRB*19
Bola-DQB1*1A
Bola-DQB2*02B
Bola-DQB1*05
Bola-DQB1*02


D
0.6
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MAAP
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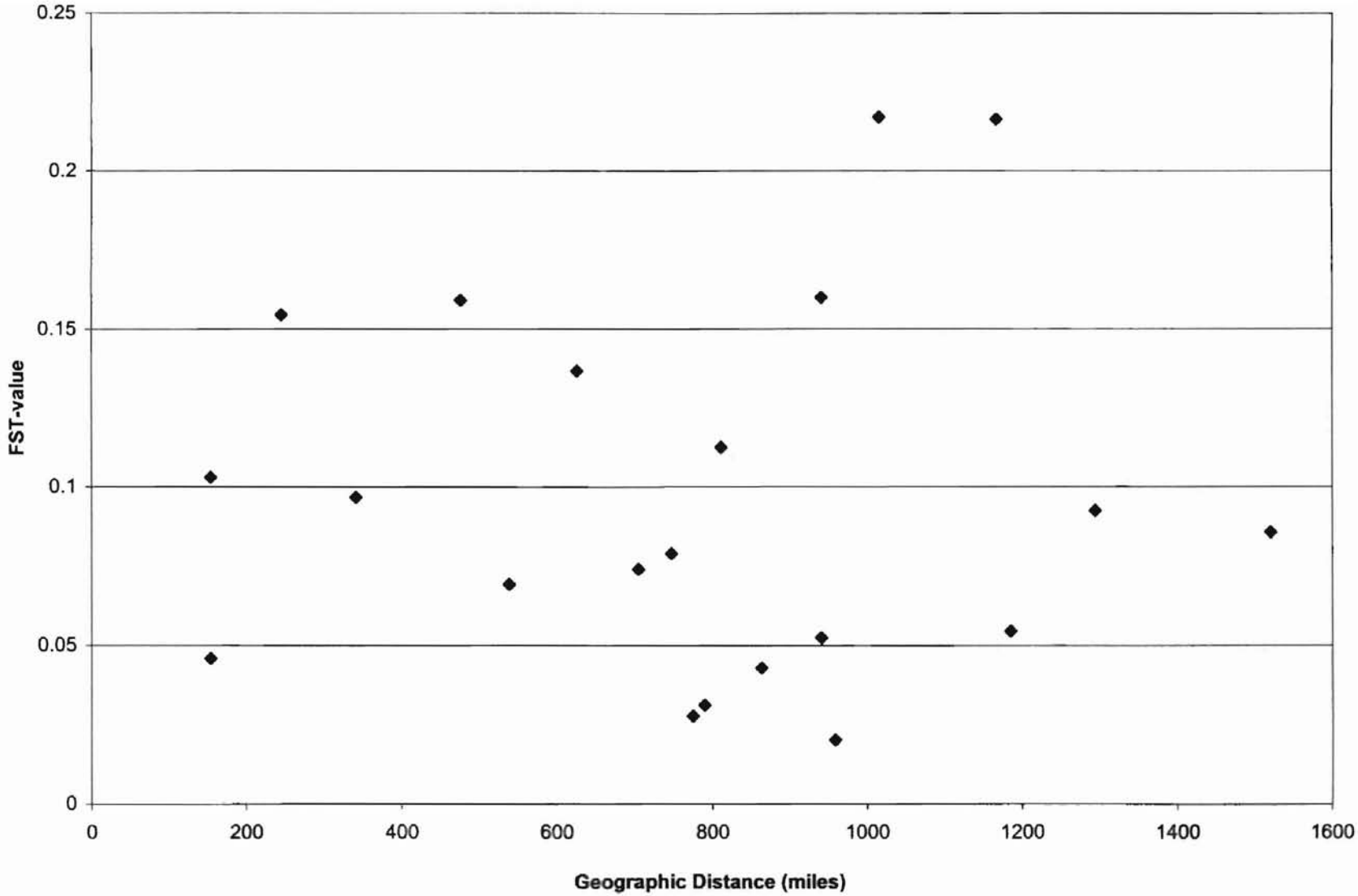
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0.2
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0.1
0.05
0
FST-value
0
200
400
600
800
1000
1200
1400
1600
Geographic Distance (miles)

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