GENETIC VARIATION IN SCELOPORUS UNDULATUS: EFFECTS OF GENE FLOW, ISOLATION, AND SELECTION

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PREFACE

Abstract

The ability of a river to alter gene flow in the lizard Sceloporus undulatus was investigated. The Cimarron River of northern Oklahoma was found not to be a barrier to gene flow but instead may actually facilitate movement within this species. Populations from alternate sides of the river were not genetically different whereas populations from the river's edge were found to be more genetically homogenous than inland populations, indicating that gene flow is enhanced in riverine areas. This gene flow along the river tends to be asymmetric in the direction of the river's current, possibly aided by rafting of lizards or their eggs downstream during floods. Two factors which appear to promote differentiation in this species are the magnitude of geographic distance between populations and differences in habitat. An east-west genetic cline was demonstrated, and coincides well with a similar cline in habitat. In addition, far eastern Oklahoma samples consisting of pure S. u. hyacinthinus were found to be strongly differentiated from all other samples, indicating that this subspecies is genetically quite different from S. u. garmani.

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CHAPTER I

INTRODUCTION

Uninhibited gene flow tends to maintain species identity, and if interrupted, will allow populations to diverge independently of one another (Dobzhansky 1937, Mayr 1942, Futuyma 1979). A geographic barrier such as a river, canyon, or mountain range may serve as such an isolating mechanism (Stebbins 1949, Blair 1950, 1953, Willey and Willey 1967, Rees 1970, Gill 1976, Power 1979). Pounds and Jackson (1981) showed that a river may serve as a geographic barrier to gene flow for the lizard Sceloporus undulatus.

The present study investigates the effects of the Cimarron River, which traverses northern Oklahoma from west to east, on gene flow in S. undulatus. Populations on each side of the river were compared for genetic differences. Barring selection, these differences could suggest that the river serves as a barrier to gene flow in S. undulatus. Additionally, populations near the river were compared to populations inland. Increased homogeneity along the river might suggest increased gene flow along the river if selection pressures are equal. Finally, gene flow along the river could be asymmetrically skewed in the direction of the

river's current. This is feasible due to a strong ecological association of the lizards to log piles along the riverbank, which may provide a means of rafting the lizard downstream during floods. Patterns of genotypes along the river compared to adjacent inland sites were analyzed to test this hypothesis of asymmetric downstream gene flow near the river.

CHAPTER II

LITERATURE REVIEW

Geographic Barriers to Gene Flow

When populations are free to exchange genetic information with one another, the gene pool remains homogeneous and cohesion within the species is maintained (Dobzhansky 1937, Mayr 1942, Futuyma 1979). Such sustained gene flow may inhibit divergence despite disparate selective pressures (Camin and Ehrlich 1958). Other investigators have shown that differentiation within a species is inversely related to the amount of gene flow within that species (Rees 1970, Jackson 1973). Therefore, gene flow seems to inhibit differentiation by maintaining genetic cohesion (Futuyma 1979). This de-differentiating effect of gene flow is sometimes referred to as the neo-Darwinian view of gene flow (Jackson and Pounds 1979).

Gene flow may be blocked by geographic barriers such as rivers, canyons, mountain ranges, etc. (Stebbins 1949, Blair 1950, 1953, Willey and Willey 1967, Rees 1970, Gill 1976, Power 1979). If such a barrier isolates one part of a population from another, divergence will occur as each

population changes independently of the other due to differing selective pressures and/or genetic drift. If these populations were then reunited at a later time, enough divergence may have taken place so that the two populations will be genetically incompatible or will produce hybrids which are adaptively obsolete in either parental environment (i.e. postmating isolating mechanisms). Selection would then favor those individuals who mated only with individuals from their own parental population (i.e. premating isolating mechanisms).

Such reproductive isolation initiated by changes while in allopatry and reinforced by subsequent sympatry has been demonstrated in natural populations (Littlejohn and Loftus-Hills 1968, Huey and Pianka 1974), and shown experimentally (Knight et al. 1956, Kessler 1966). Therefore differentiation, and eventually speciation, can result from disrupted gene flow. This is the classic concept of allopatric speciation which was challenged by Ehrlich and Raven (1969). Ehrlich and Raven contend that selection is both the cohesive and disruptive force in nature and that gene flow serving as a cohesive force is not as rampant as commonly thought. In debating this point, Ehrlich and Raven used several subjective examples backed by little empirical evidence. Even so, their opinion was embraced by a significant portion of biologists. In a critical review of this subject, Jackson and Pounds (1979) postulate that Ehrlich and Raven's paper, while written to provoke research, was instead accepted indiscriminately.

Another often-cited proponent of Ehrlich and Raven's view is Endler (1973, 1977). Given a smooth clinal gradient of selection, Endler showed that gene flow, in both laboratory and modeling experiments, did not have a homogenizing effect. When gene flow from adjacent demes is equal, the effect of immigrating genes will be neutralized and a genetic gradient is maintained in spite of significant gene flow. When gene flow is asymmetric, a lateral shift in the genetic cline is produced. Such an asymmetry could shift the geographic location of a cline adapted to a selection gradient towards the direction of greatest gene flow. In these experiments, Endler subjected gene flow to constraints rarely achieved in nature, and observed differentiation in only one character or at a single locus. This is unrealistic in that many gene interactions are complex. In addition, the possibility of polygenic inheritance or pleiotropy is bypassed when only one locus is evaluated. Endler also constrained his experiments to fit a smooth clinal gradient of selection, and these are rare in nature given that the environment is in constant flux and may be patchier than Endler asssumes. Endler also emphasized that selection is capable of overpowering gene flow. While this is not disputed, today's literature lacks empirical evidence to rule out gene flow as an important factor maintaining species identity. Field studies are required to investigate this issue. Once these are accomplished, questions about the frequency and magnitude of the selective force required to overcome gene flow can then be examined.

Geographic barriers frequently serve as isolating mechanisms in natural populations (Stebbins 1949, Blair 1950, 1953, Willey and Willey 1967, Rees 1970, Gill 1976, Power 1979). If populations separated by such barriers have similar selective forces acting upon them, then genetic drift may play a more prominent role in differentiation than previously thought. Speith (1974) demonstrated that only one immigrant per generation was required to counteract drift. Later, Allendorf and Phelps (1981) showed that statistically significant allelic divergence may be present even when more than one individual per generation is exchanged among subpopulations, but as the number of migrating individuals increased, the chance of statistically significant divergence decreased. Although some populations may consist largely of sedentary individuals, there may exist a smaller portion of individuals with greater dispersal tendencies (Tinkle 1969, Kiester 1982). The tendency to disperse may also be greater only during certain stages of a sedentary organism's life cycle, such as nesting excursions by females, or home range changes by juveniles of some iguanid lizards (Kerster 1964). Therefore, many populations may easily receive sufficient immigration each generation to overcome genetic drift. To study the effect of genetic drift one must study populations which undergo severely restricted gene flow, such as those isolated by a geographic barrier. By studying the populations on each side of the barrier, and by assuming equivalent selection pressures on each side of the barrier, populational

differences can be attributed to a lack of gene flow. Pounds and Jackson (1981) showed that populations of the lizard Sceloporus undulatus diverged morphologically in response to riverine barriers to gene flow. Pounds and Jackson's experimental design, however, failed to control for the effects of habitat differences near to vs inland from the river.

Natural Selection

Ever since Darwin's On the Origin of Species (1859) biologists have sought indisputable examples of natural selection. One of the best-known cases of natural selection is that of industrial melanism (Kettlewell 1955, 1956). Black morphs of a predominantly white moth species (Biston betularia) experienced a selective advantage on soot-covered trees in areas exposed to industrial pollution. The selective agent acting on the moths was differential predation by birds. Previous to the age of industrialism, the white morph had experienced a selective advantage on white lichen-covered trees and still does in unpolluted areas (Kettlewell 1973). Another oft-cited example of selection-induced variation is shell color and banding pattern in the land snail, Cepaea nemoralis (Cain and Sheppard 1954, Clarke 1960). Snails which did not match the color and banding pattern of their background habitat experienced increased predation by thrushes (Sheppard 1951).

Today, the body of literature devoted to natural selection and its association with various environmental parameters continues to increase (Arnold 1969, Fox 1975, 1978, 1983, Price and Grant 1984, Price et al. 1984, Alatalo and Lundberg 1986, Smith 1986). An attempt to gauge the importance of other factors affecting genetic variation in the absence of natural selection promoted the use of electrophoresis. It was first proposed that enzymes maintained a similar enzymatic action in their various isozymic forms. Thus, it was assumed that the isozymes were selectively neutral entities in response to environmental pressures (Fuerst et al. 1977). More recently, however, various isozymes of a given enzyme have been associated with a selective advantage (Christiansen et al. 1973, Tinkle and Selander 1973, Mitton and Koehn 1975, Koehn et al. 1976, 1980, Koehn and Williams 1978, Nevo et al. 1986). Therefore, the effect of natural selection must be considered when assessing genetic variation in electrophoretic studies.

Several investigators have tried to separate the effect of natural selection from that of gene flow. Camin and Ehrlich (1958) showed that the effect of gene flow could overcome color-pattern selection in water snakes (Nerodia). Conversely, selection has also been shown to overcome the effect of gene flow (Endler 1973). Therefore, the effect of natural selection should always be assessed in any study of gene flow.

Variation Due to Geographic Distance

Although gene flow between adjacent populations may have a homogenizing effect, slight variation in gene frequencies between two or more regions may still result in a geographic cline or gradient (Huxley 1939). Even when the gene flow is significant, the genetic gradient of the cline may be maintained by the neutralizing effect of equal immigration from adjacent demes (Endler 1973). However, if gene flow is asymmetrical, the cline shifts in the direction of increased gene flow (Endler 1973). Genetic variation along the cline may coincide with selective pressures resulting from environmental discontinuities such as variation in soil types, plant types, moisture, and plant formations (Miller 1956). In addition, a cline may become steeper where selective pressures are especially strong (Antonovics and Bradshaw 1970, Antonovics et al. 1971). Therefore, the genetic frequencies in any one region are an average of selective pressures of adjacent regions to which genes are exposed (Futuyma 1979). Dissimilarities along the cline may then be due to cumulative changes that have taken place between various regions (Goldschmidt 1940, Kruckeberg 1957, and Oliver 1972). Therefore, though populations may be locally indistinguishable due to gene flow, geographically distant populations along the cline may be genetically very different.

The Study Organism

Four subspecies of *Sceloporus undulatus* occur in Oklahoma (Figure 1). *S. undulatus garmani* was the main subspecies of interest in this study, although its genetic relationship to *S. undulatus hyacinthinus* was also investigated. These lizards are abundant and may be found in any area that provides suitable microhabitat. They are often situated on the edges of wooded areas which provide open sun, sufficient refuges, and trees. *S. u. hyacinthinus* inhabits the eastern third of the state and *S. u. garmani* inhabits most of the rest of the state except the southwest corner and much of the panhandle. These two subspecies form an intergrade zone where their ranges meet (Figure 1). Differences in the pattern and morphology of these subspecies provide an easy means of identification: *S. u. garmani* has distinct dorsolateral whitish stripes bordered medially by brownish spots (Figure 2), whereas *S. u. hyacinthinus* lacks the dorsolateral stripes but has narrow, undulate, dark-brown crossbands instead (Figure 3) (Webb 1970). This species is ideal for a study of riverine effects on gene flow due to the low probability of it fording a river and because it is abundant across Oklahoma. In addition, the intergrade zone for the two subspecies is an ideal area in which to characterize gene flow along a cline connecting two potentially interbreeding subspecies.

CHAPTER III

OBJECTIVES

The iguanid lizard Sceloporus undulatus was selected to study riverine effects on gene flow. The following objectives were proposed:

1) To determine if a river can serve as a barrier to gene flow in S. undulatus,
2) To determine if gene flow is enhanced along the riverine border compared to inland sites,
3) To determine if gene flow is augmented in the direction of the river's current,
4) To quantify the extent of population variation due to other factors such as natural selection and geographic distance,
5) To reveal genetic differences between S. u. garmani and S. u. hyacinthinus.

The primary hypothesis of this study was that the Cimarron River, which traverses northern Oklahoma from west to east, is a barrier to gene flow in populations of S. undulatus. Objective (1) would test the hypothesis proposed by Pounds and Jackson (1981) that a river can inhibit gene flow in S. undulatus. In addressing this question, lizards

from each side of a river were genetically compared by the use of starch-gel electrophoresis.

Subsidiary objectives (2) and (3) were not previously addressed in the literature and deal with a river's influence on terrestrial population structure and gene flow. The habitat along the river's edge is generally more continuous and homogenous than the inland habitat, and may therefore facilitate animal movements. At each study site, inland and riverine populations were sampled. To address objective 2, variability among inland populations was compared to that among riverine populations separately for each side of the river. Furthermore, gene flow may be enhanced downstream as per objective (3). Those lizards which inhabit the floodplain along the river are exposed to frequent, often dramatic floods. During floods lizards and/or their eggs may be swept downstream or carried downstream on floating logs (Smith 1946). This would create asymmetric gene flow in the direction of the river's current. If an east-west geographic cline existed in any of the electrophoretic traits, then the cline should shift eastward among the riverine populations in the direction of the asymmetric gene flow (Endler 1973). Such river-enhanced gene flow has not been demonstrated before in any terrestrial vertebrate, although it has been observed in fish (Echelle et al. 1976). Electrophoretic data were examined to determine if first, there existed a geographic cline in allelic frequencies, and second, whether it shifted in the downstream direction along the river's edge as

compared to inland samples.

In addressing objective 4, population variation was examined to determine whether observed variation was due to sources other than the river itself; such as natural selection, genetic drift, and variation due to geographic distance. The effect of natural selection was evaluated by correlating variation in habitat parameters to variation in genotypic frequencies. If habitat and genotypic variation coincided, then it is likely that habitat differences were exerting selective pressures on the genetic structure of the populations. The effect of genetic drift was assessed by examining electrophoretic data for random variation as opposed to consistent trends in allelic frequencies. Variation due to geographic distance was assessed by comparing the magnitude of genetic differentiation between populations to the magnitude of geographic distance between them.

Finally, patterns of allelic frequencies were examined for genetic differences between S. u. garmani and S. u. hyacinthinus. Genetic distances (Wright 1978) were derived to serve as a useful index of subspecific differentiation.

CHAPTER IV

MATERIALS AND METHODS

Lizards were collected from both sides of the river at four sampling sites equidistant along the river as follows:

1.) Kingfisher Co., 8.5 km. southeast of Dover, OK,

2.) Logan Co., 11 km. north of Guthrie, OK,

3.) Payne Co., 3 km. south of Ripley, OK,

4.) Creek Co., 3 km. northwest of Silver City, OK.

Each site was separated from the next adjacent site by 65 river-kilometers (Figure 4). At each of the collection sites, four samples of twenty lizards apiece were collected as follows:

1.) Along the north side of the river, (north riverine),

2.) 1.6 km. inland on the north side of the river, (north inland),

3.) Along the south side of the river, (south riverine),

4.) 1.6 km. inland on the south side of the river, (south inland) (Figure 5).

Therefore, each sample came from one of four counties,

either north or south of the river, in either riverine or inland habitat. Reference to collection sites is by a three letter sequence:

1) The first letter specifies the county (from west to east: Kingfisher (K), Logan (L), Payne (P), and Creek (C),

2) The second letter designates north (N) or south (S) of the river,

3.) The third letter denotes inland (I) or riverine (R).

In addition, two extra collections were conducted: one far east (Rocky Ford State Park in Cherokee Co.) and the other far west (Little Sahara Recreation Area in Woods Co.). These two collections represented pure forms of the two subspecies and aided in distinguishing east-west clinal trends. These collections are referred to in the following text as the east and west collections.

Lizards were captured by noosing, blowgunning, or hand, and were transported to the laboratory in an ice chest. The lizards were labeled according to their site of collection and then frozen at -60 C. Later, the lizards were thawed slightly to remove tissue for electrophoresis.

Preliminary electrophoretic surveys were conducted to determine the best gel buffer system , enzymes, tissue, and stain types to use in further analyses. In general, the techniques and buffers follow Selander et al. (Appendix A).

It was found that tail muscle provided the best electrophoretic resolution and so was utilized in all electrophoretic trials. The two gel types principally used were tris-citrate (pH = 6.0) and lithium hydroxide (pH = 8.0). Initial trials included the assay of the following 14 enzymes: esterase (EST), indophenol oxidase (IPO), 6-phosphogluconate dehydrogenase (6-PGD), glucose phosphate isomerase (GPI), (GPD), malate dehydrogenase (MDH), lactate dehydrogenase (LDH), general protein (GP), alkaline phosphatase (AKP), glycerophosphate dehydrogenase (GPD), glutamic oxylate transaminase (GOT), isocitrate dehydrogenase (IDH), phosphoglucomutase (PGM), and mannose-6-phosphate (MPI). These enzymes were known to be polymorphic and useful in evaluating geographic variation within S. undulatus and other closely related species (Spohn and Guttman 1976, Wyles and Gorman 1978). Enzymes found to be either monomorphic or inconsistent in their staining were discarded from further analyses. Multiple isozymes of enzymes were designated numerically with the locus migrating furthest from the gel origin being "1" and the slower locus "2". Alleles were labeled alphabetically for ease in scoring.

Five enzymes (PGM, MPI, LDH, MDH, and GOT) were retained for statistical analyses. Various statistical tests and programs such as BIOSYS-1 (Swofford and Selander 1981), Mantel (Douglas and Endler 1982) principal components analysis (Pierce and Mitton 1980), Wilcoxon rank sum test (Ott 1977), and the simultaneous test procedure (STP) (Sokal

and Rohlf 1969) were employed.

A habitat analysis was conducted to assess potential environmentally-imposed selection pressures. Four transects of 29.3 m. by 1.7 m. were sampled at each collection site. Two of the transects traversed areas in which lizards had been sighted or caught, and so were labeled "biased" transects. The other two transects (random) crossed the center of the collection area, perpendicular to one another, and may or may not have traversed areas in which lizards were sighted. All trees, shrubs, and log piles were counted in each transect. The tree category consisted of any plant fitting the botanical definition of a tree: a woody, perennial plant with a single main trunk bearing lateral branches with few or no branches persisting from the base (Usher 1966, Holmes 1979). Shrubs included salt cedars (genus:Tamarix) and any plant fitting the botanical definition of a shrub: a woody plant in which well-developed side shoots branch from the base so that there is no main trunk (Usher 1966, Holmes 1979). Any dead or fallen trees were included in the log pile category. These structures were chosen because they seem to be integral parts of a lizard's habitat which may afford a selective advantage. Logs are associated with increased food availability (Ferguson et al. 1983) while trees, shrubs, and log piles all provide a refuge from predators and weather, as well as a thermoregulatory structure. Since S. undulatus tends to be quite arboreal, trees and log piles are an especially important component of its habitat.

In addition, five other habitat features were graded subjectively as follows:

1. Grass, herbacious plants, and ground litter were estimated to be absent (1), sparse (2), few (3), moderate (4), many (5), or abundant (6).

2. Canopy cover was estimated to be 100% (1), 80% (2), 65% (3), 50% (4), 25% (5), 0% (6).

3. Soil was categorized as clay or dark loam (1), sandy loam (2), very sandy loam (3), pure sand (4).

These subjective data may be important to a lizard's motile capabilities within its environment. Hypothetically, dense grassy patches, litter, and abundance of herbacious plants might inhibit a lizard's movement to surrounding areas, while sand might facilitate it. In addition, areas exposed to open sun for the majority of the day attract high densities of S. undulatus (Ferguson et al. 1983). All study sites were assayed in spring (April) of 1985, and lizards were captured in the summer of that and the previous year. Only one lizard could be caught at the Creek south riverine site, resulting in the selection of a new site 14.5 km. upriver. Since the new site was selected in fall of 1985, no habitat data had been collected for it. Therefore, in spring of 1986 the new Creek south riverine site was sampled and the old Creek south riverine and Creek south inland sites were re-sampled. The new data on the old sites were then used in between-year comparisons. No differences

between years were found for trees, shrubs, or log piles by an analysis of variance (ANOVA). Therefore, the old Creek south riverine data were replaced with the new Creek south riverine data in further analyses of these quantitative data. However, differences were found between years for the subjective data, disallowing the exchange of the new Creek south riverine data for the old. In further analysis of these data only northern areas were utitlized.

CHAPTER V

RESULTS AND DISCUSSION

Genetic Results

Five enzyme systems (PGM, MPI, LDH, MDH, and GOT) were retained for statistical analyses. Of these, LDH and MDH each exhibited two isozymes so that seven loci were assayed altogether. LDH-1 and MDH-1 showed no genetic variation, MDH-2 and GOT displayed rare variation, while PGM, MPI, and LDH-2 were most variable (Table I). All but three samples (East for LDH-2, CSR for PGM, and CNR for PGM) did not deviate significantly from Hardy-Weinberg expectations for each locus. Geographic patterns of allelic frequencies (Figures 6, 7, and 8), genetic distances (Wright 1978), and genetic similarities (Nei 1978) (Table II) were examined for across-river differences, clinal trends, near river homogeneity, and subspecific differences.

Riverine Barrier to Gene Flow

Two analyses utilizing all loci were performed to test for genetic differentiation on alternate sides of the river.

The first used Wright's F statistics (Wright 1969) in which Fst values provided a measure of heterogeneity among subpopulations. Genetic heterogeneity of the total population, north populations, and south populations were compared to determine if the Cimarron River was indeed a barrier to gene flow. Total population heterogeneity (Fst = .082) was similar to that from either the northern (Fst = .063) or the southern (Fst = .083) populations (Figure 9). In assessing the inland and riverine populations alone, total heterogeneity of the inland populations (Fst = .092) was again similar to that of the north inland (Fst = .077) and the south inland (Fst = .087) populations. Likewise, heterogeneity of all riverine populations (Fst = .068) was roughly equivalent to the north riverine (Fst = .049) and the south riverine (Fst = .069) populations taken singly (Figure 9). Therefore, the F statistics indicate the river is not a barrier to gene flow.

The second analysis utilized pairwise genetic distance scores. Genetic distance scores of all pairs of populations from the same side of the river were compared to the genetic distance scores of all pairs of populations from opposite sides of the river (Table III) using a Wilcoxon rank sum test (Ott 1977). Genetic distances spanning the river were not significantly different from distances on the same side of the river ($Z = -0.7996$, $N1 = 64$, $N2 = 56$, $p > .05$).

Analyses utilizing one locus at a time were also performed to evaluate genetic differentiation across the

river. The first, a simultaneous test procedure (STP) (Sokal and Rohlf 1969), groups homogeneous populations and allows the detection of divergent populations or groups of populations. Only the polymorphic enzymes (LDH-2, MPI, and PGM) were used in this test. Rare alleles were grouped with the next most frequent allele. Populations were ranked with respect to the frequency of the most common allele and homogeneous subgroups of allelic frequencies for each locus were identified. Two homogeneous subgroups divergent from each other were delineated for each locus. Considerable overlap and homogeneity were exibited among populations and no clear genetic differentiation across the river was apparent in any enzyme (Figures 10-12). Again, the river seems to be an ineffective barrier to gene flow.

Finally, genotypic frequencies for each enzyme across the river were compared by chi-square heterogeneity tests. Due to significant variation among samples from various counties, chi-square heterogeneity tests were conducted for each county individually. LDH-2 exibited significant variation only in Kingfisher and Payne counties (X^2 = 8.088, df = 2, $p < .02$ and X^2 = 13.695, df = 2, $p = .001$, respectively) (Tables IV and V). In addition, MPI exhibited significant across river variation in Logan and Creek counties (X^2 = 5.55, df = 1, $p < .02$ and X^2 = 8.613, df = 2, $p < .02$, respectively) and PGM showed across river variation in Creek county (X^2 = 7.172, df = 2, $p < .03$) (Tables VI-VIII). The minimum of five expected observations per class prescribed by chi-square tests has been shown to be

unnecessarily restrictive (Roscoe and Byars 1971). Instead, an average of six expected observations per cell is adequate to maintain test validity at the α = 0.05 level. Though not all chi-square analyses met the five observation per cell criterion, all fulfilled the minimum average of six observations per cell requirement.

Of all the analyses, only the latter chi-square tests suggest some genetic differences across the river. These across-river differences in genetic frequencies are probably not due to the river itself because they are not consistently seen in all counties or in all enzymes. The observed population diferences in LDH and MPI are probably due to some other factor such as selection pressures to their specific micro-localities or random forces. Taken together, all analyses indicate little differentiation on alternate sides of the river and fail to support the river as a barrier to gene flow.

Genetic Differentiation by Distance

Although little genetic differentiation was noted across the river, it was apparent from inspection of allelic frequency data and the STP results that variation existed in an east-west direction along the river (Figures 6-8 and 10-12). Two aspects of this differentiation will be discussed: 1) variation due to distance and 2) clinal trends between two subspecies.

Differentiation due to geographic distance was first quantified by comparing pairwise genetic distances with the corresponding geographic distances using the Mantel test (Douglas and Endler 1982). A significant correlation between geographic and genetic distances was seen ($T = 5.024$, $p = .01$). This indicates that populations are genetically different from one another primarily through the geographic distances separating them.

Because of the tortuous path of the Cimarron River, some of the sample sites are further north or south than others. Despite the uniform collecting design along the river, the increased genetic variation with increased geographic distance may be due in part to latitudinal differences. To filter out latitudinal effects, each geographic distance measure was partitioned into its two corresponding east-west and north-south vectors. Differences in latitudinal (north-south) distance between all pairs of populations as well as longitudinal (east-west) distances between pairs of populations were measured and each matrix was compared against the matrix of genetic distances, by the use of the Mantel test. No correlation was found between latitudinal geographic distances and genetic distances ($T = 0.026$ $p>.05$) but a correlation was found between longitudinal geographic distance and genetic distance ($T = 5.038$, $p = .01$). Therefore, the positive relation between genetic differences and geographic distance is due to the east-west component of distance and not the north-south component.

To further explain the variation noted with increased geographic distance, as well as that contributed by gene flow between subspecies, a principal component analysis of allelic frequencies was conducted (Pierce and Mitton 1980). Principal components analysis (PCA) is a multivariate method to condense many variables into fewer principal axes (eigenvectors) which should explain most of the variation in the data set. Allelic frequencies (Table I) were the variables for this analysis. When a locus had two alleles only the frequency of one was included since the frequency of the second allele is redundant information. If more than two alleles were present for a locus, each allele was included in the analyses since any one allele would not necessarily covary with either of the remaining alleles. Most of the variation in the data (99.5 %) can be explained by the first four components (Table IX). Factor loadings are the correlation of the variables with each axis and represent the contribution of each variable to a particular axis. Of these, LDH-2-A, and PGM-A loaded highly and negatively on the first principal component axis while LDH-2-C and PGM-C loaded highly and positively (Table IX). LDH-2-A and PGM-A loaded highly due to their abundance in western populations as compared to the far eastern population, while LDH-2-C and PGM-C loaded highly due to their abundance in the eastern population compared to all other populations (Figures 6 and 7). The eastern population consists of pure S. u. hyacinthinus; all other populations can be considered S. u. garmani. Principal component 1 thus

separates S. u. hyacinthinus from S. u. garmani (Figure 13). Nevertheless, eastern populations (C and P) fall out mainly positively on the first principal component axis while the western populations (L and K) fall out negatively. Although this axis mainly expresses the genetic differences between the two subspecies, the genetic affinity of the easternmost S. u. garmani populations with pure S. u. hyacinthinus is also indicated. Gene flow between these two subspecies probably accounts for the observed genetic intermediacy of the study populations between the east and west samples.

The second principal component loads highly and positively for PGM-A and highly but negatively for PGM-B. Thus, these two alleles form a cline from west to east in which PGM-A decreases as PGM-B increases (Figure 7). Due to the lack of the "B" allele in the far eastern population, the subspecific differentiation is not important in this component. The second principal component expresses the genetic variation within populations of S. u. garmani in the form of a geographic cline from west to east. Eastern counties (Creek and Payne) fall out negatively on the second principal axis while western counties (Kingfisher and Logan) fall out positively, forming a visualization of the cline (Figure 13).

Finally, a cluster analysis of genetic distances using the unweighted pair-group method (Sneath and Sokal 1973) was conducted (Figure 14). The far eastern population distinctly separated from all other populations, further

confirming the genetic disparity between the subspecies. Next, the far western population branched off followed by the remaining samples which formed two major groups. One group consisted of samples from Creek and Payne counties (eastern counties), while the other contained samples predominantly from Logan and Kingfisher counties (western counties).

In conclusion, the Mantel test, PCA, and cluster analysis indicate differentiation with increasing longitudinal distance. The PCA partitioned this variation such that the first principal component distinguished differences between subspecies whereas the second component described micro-geographic variation within a sub-species in the form of a gradual genetic cline.

Homogeneity of the Riverine Populations

Two effects of the river on lizard populations inhabiting areas along the river's edge were investigated: 1) the amount of population homogeneity along the river compared to inland, and 2) the ability of the river to facilitate gene flow downstream.

The enhancement of gene flow along the river's border compared to inland sites was first assessed by the use of Fst statistics. Heterogeneity of the inland populations (Fst = .092) was greater than that of riverine populations (Fst = .068). This trend persisted when the collections

were subdivided further. North riverine populations (Fst = .049) were more homogeneous than north inland populations (Fst = .077), as were south riverine populations (Fst = .069) compared to south inland populations (Fst = .087) (Figure 9). Although the magnitude of differences between these values is not large, it is noteworthy that the inland Fst values are not only higher than riverine values, but they are also larger than the total population Fst in two out of four cases.

To further quantify this difference a Mantel test was conducted in which genetic distance and geographic distance were compared for inland and riverine populations separately. A significant association between genetic distance and geographic distance was found for the inland ($T = 3.308$, $p < .01$) but not the riverine populations ($T = 1.653$, $p > 0.05$). Therefore, more genetic differentiation with distance was seen inland than immediately along the river.

Both the Fst and the Mantel results indicate that riverine populations appear to be more homogeneous than the inland populations. In assessing the significance of this variation, a Wilcoxon Rank Sum test (Ott 1977) was conducted. The genetic distance scores for pairs of populations from the same type of area (inland with inland and riverine with riverine) and from the same side of the river (south with south and north with north) were compared (Table X). The difference in the genetic distance scores

from these habitats is significant by a one-tailed test ($Z = 1.7621$, $p<.04$), indicating greater homogeneity among riverine populations than populations 1.6 kilometers inland. Genotypes from inland populations were directly compared to riverine populations by the use of heterogeneity chi-square tests. Significant differences were noted for PGM in Payne county ($X = 10.930$, $df = 5$), MPI in Logan county ($X = 5.145$, $df = 1$), and LDH in Logan county ($X = 9,227$, $df = 2$).

Riverine populations thus tend to be more homogenous than inland populations though not uniformly across all counties. Habitats may be different in the different counties so that gene flow may be facilitated between riverine and inland sites in some counties but not others. In any case, it appears that gene flow is more important right along the river than in upland sites.

As to whether this trend of enhanced gene flow along the rivers' edge is directional, patterns in allelic frequencies, STP tests, and PCA indicate that it may be. The Cimarron River flows from west to east in northern Oklahoma. Populations sampled along the river and inland from it exhibited east-west differences indicating a geographic cline. When gene flow is asymmetric along a geographic cline, a lateral shift towards the direction of increased gene flow will result. Therefore, if the river acts to facilitate downstream gene flow during floods, an eastward shift in a geographic cline should appear near the

river, where asymmetric gene flow is hypothesized, but not inland. Visually, allelic frequencies typical of the west should persist further east directly along the river, funneled by increased gene flow downstream there.

The PGM enzyme provides the best example of a geographic cline as is apparent from its high loadings on the second principal component in the PCA. The STP test for PGM (Figure 10) shows increased homogeneity farther eastward in riverine sites than inland sites thus indicating an eastward shift in the genetic cline along the river and suggesting downstream gene flow.

Examination of allelic frequencies for PGM reveals a decrease in the "A" allele from west to east (Figures 7 and 15). If the river does facilitate downstream gene flow, then the occurrence of this allele should persist farther east in riverine areas but not inland. Such a trend is indicated by comparison of the allelic frequencies from corresponding riverine and inland sites. In six out of eight instances the frequency of the "A" allele is greater in riverine areas than inland (Table I and Figures 7 and 15).

Another look at the principal components analysis also indicates that downstream gene flow occurs. Propagation of gene flow downstream should serve to increase similarity between riverine populations and their immediate western neighbors. Six out of the the eight riverine populations show a tendency to fall to the west (i.e. more positively on

the second principal component) than their inland counterparts (Figure 13).

In conclusion, both multivariate analysis of geographic patterns of all loci taken together and clinal patterns of PGM in particular serve to illustrate downstream gene flow in riverine areas. This downstream shift was indicated by the persistent occurrence of a geographically decreasing allele, increased homogeneity of riverine populations, and increased affinity to western populations as compared to their inland counterparts.

Natural Selection

Habitat analysis

The effect of natural selection can often be assessed by differences observed in the habitats of variable populations (Sheppard 1951, Arnold 1969, Antonovics and Bradshaw 1970, Kettlewell 1973, Fox 1975, Price et al. 1984, Alatalo and Lundberg 1986, Smith 1986). Two types of habitat data will be discussed: 1) quantitative data based on the density of trees, shrubs, and log piles, and 2) qualitative or subjective data based on the relative abundance of grass, herbage, litter, canopy cover, and soil type. The biased transects were used in habitat analyses because these represent typical microhabitat of the lizard.

For all sites, analysis of variance (ANOVA) and Duncan's multiple range tests were used to compare the densities of trees, shrubs, and log piles between areas north and south of the river, between inland and riverine habitats, and among the four counties. In all comparisons, neither across-the-river differences, nor inland to riverine differences were noted for trees, shrubs, or log piles. In addition, no among-county differences were seen in shrubs or log piles, but a significant difference was noted in tree density ($F = 4.39$, $df = 3$, $p < .02$). Duncan's multiple range test of the means was used to determine in which counties the differences occurred. Not surprisingly, the number of trees increases as one moves eastward in Oklahoma with Creek and Payne counties grouping together and Logan and Kingfisher counties grouping together. The data conform to the known vegetational patterns of the state in that western Oklahoma is more prairie-like and eastern Oklahoma is more wooded (Figure 16).

In assessing the subjective data, differences were noted for the amount of herbage and litter among counties ($F = 4.67$, $df = 3$, $p < .04$ and $F = 4.68$, $df = 3$, $p < .04$, respectively). Duncan's tests were performed on these data but clear east-west patterns were not discernable. These characteristics tend to be more patchy than clinal. Since a clinal pattern is apparent in the genetic data but not the subjective habitat data, they are probably unrelated.

Inland-to-riverine differences were noted for grass,

litter, and soil ($F = 5.76$, $df = 1$, $p < .04$, $F = 7.35$, $df = 1$, $p < .03$ and $F = 16.20$ $df = 1$, and $p < .01$, respectively). Comparing the means with the Duncan's test showed a significantly higher amount of grass (inland $\bar{X}= 4.75$; riverine $\bar{X} = 3.375$) and litter (inland $\bar{X} =4.5$; riverine $\bar{X} = 2.875$) in inland than riverine areas. In addition, riverine areas showed a higher incidence of sandy soil than inland (inland $\bar{X} = 2.375$, riverine $\bar{X} = 3.5$). These results are intuitive when considering the overall riverine and inland environments. A decreased amount of grass and litter along with a more sandy soil could serve to facilitate lizard movement in riverine areas, thus helping to explain the enhanced gene flow there.

Comparisons of Juveniles and Adults

To assess the effects of natural selection on a population one could compare characteristics of juveniles to adults in a population (Hecht 1951, Fox 1975). It could then be assumed that differences between these groups represent the selective pressures acting on an organism before it reaches maturity. Selective pressures acting on S. undulatus are very high, especially within the first year of life (Ferguson et al. 1980, 1983), so that this lizard serves as a model organism in which selection can be observed.

Approximate age estimations in Sceloporus may be determined from snout-vent lengths (SVL) (Ferguson and Brockman 1980). A snout-vent length of 40 mm was chosen as the limit between juveniles and adults (Fitch 1970, Tinkle and Ballinger 1972, Ferguson et al. 1980). Differences between juvenile and adult genotypes were then compared using heterogeneity chi-square tests. Due to east-west differences among samples from various counties, Chi-square analyses were conducted on data from each county separately. No overall genotypic differences were noted for any enzyme in any county when comparing adults and juveniles (Table XI). Therefore, selection doesn't seem to be acting upon lizards between these age classes.

The same type of analysis was conducted for hatchlings compared to adults. A hatchling is a lizard less than a month old with a SVL less than 30 mm (Fitch 1970). Chi-square analyses by counties revealed a significant difference between hatchlings and all other lizards from Kingfisher county for MPI (X^2 = 12.884, df = 2, $p < .01$) and in Payne county for PGM (X^2 = 10.222, df = 2, $p < .01$) (Tables XII and XIII). Therefore, selection may be acting on the hatchlings in these two counties. In general, selection on the enzymes of this study appears weak.

CHAPTER VI

CONCLUSIONS

It seems clear that the Cimarron River is an ineffective barrier to gene flow in S. undulatus in northern Oklahoma. On the other hand it may serve as a potential propagator of gene flow. Since populations are homogeneous by the river as opposed to inland, some factor must be aiding lizard movements there. Two possibilities are a continuous and homogeneous habitat and river-facilitated movements. The habitat is much more continuous along the river than inland. Inland areas are interspersed with abundant plowed fields, heavily grazed brush-free pastures and dense tree groves, all of which are known to be unfavorable habitat for S. undulatus (Ferguson et al. 1983) and serve to isolate these populations from one another. In addition, the habitat near the river is such that lizard mobility is made easier. Decreased amounts of grass and ground litter might aid lizard movement there. Also, the open sandy soil near the river might serve to facilitate movement so that lizards are freer to migrate and interbreed enhancing the homogeneity within these populations. Therefore, the riverine habitat serves to facilitate lizard movement while inland habitats tend to inhibit it.

From another perspective frequent floods may wash the lizards or their eggs downstream and this could also homogenize the population along the river more than upland. This hypothesis is highly plausible once one understands the habits of this lizard. It is almost always found in association with log piles and readily takes cover within them (Ferguson et al. 1983). These logs themselves could act as a source of conveyance downstream in a flood (Smith 1946, Brown and Alcala 1957). Although a flood may cause high mortality within a population, it is likely that some lizards survive and it is probable that lizards inhabiting a frequently flooded area possess adaptations (especially behavioral ones; MacArthur and Wilson, 1967) to withstand such catastrophes. For example, in one flood that inundated 75% of a study area in Kansas, 56% of the marked lizards were still recaptured (Ferguson et al. 1980). Eggs also could be transported by the river's current. The Cimarron River has a high salinity content but lizard eggs have been shown to withstand exposure to saline water (Brown and Alcala 1957, Gardner 1985, Appendix B). Thus, it is quite within reason to suspect that lizards or their eggs move downstream during floods and some survive as transplanted propagules.

The geographic pattern of multi-locus genetic variation, as well as individual loci especially PGM, strongly supports this hypothesis of downstream gene flow. Riverine populations are more similar to their immediate upstream neighbors, an allele was found to persist in riverine

populations though it was decreasing in the downstream direction inland, and populations near the river exhibited more downstream homogeneity than inland populations. In actuality, both habitat-facilitated movement of lizards and downstream propagation of genes probably occur. In any case, enhanced gene flow in the downstream direction would be expected because equal migration along the shore in both directions would be tilted by the increased movement of lizards downstream.

An east-west cline in genetic variation which increased with geographic distance was noted in this lizard species. Two phenomena may account for this clinal pattern: 1) gene flow between the two subspecies and 2) natural selection.

The Creek populations abut the intergrade zone of the eastern and western subspecies and exhibit an allele which is abundant in S. u. hyacinthinus but rare in most of the more westerly populations sampled (Table I, and Figure 7). Therefore, low levels of gene flow are probably occurring between the two subspecies. The principal components analysis supported this implication, showing a skewing of the eastern counties in the direction of the pure S. u. hyacinthinus subspecies.

A key feature often associated with a genetic cline is a habitat cline. S. undulatus hyacinthinus (the eastern subspecies) is known to be arboreal, whereas the western subspecies (S. undulatus garmani) is more adapted to sandy areas with less trees, such as prairie habitats Ferguson et

al. 1983). Tree density, more than any of the other habitat parameters measured, nicely coincided with genetic trends, with trees increasing in an eastwardly direction across the state. Coincidentally, the occurrence of populations possessing S. u. hyacinthinus traits also increases in this direction both genetically and in color and pattern (personal observation). It is probable that S. u. hyacinthinus possesses certain traits that facilitate a more arboreal lifestyle. Gene flow between S. u. hyacinthinus and S. u. garmani would serve to pass these traits on to the eastern S. u. garmani populations. These traits would then be maintained by an adaptive advantage in the wooded areas of the east. Some of these traits may have been associated with the enzymes assayed by this study. In conclusion, gene flow between the two subspecies along with compatible selection pressures probably serve to maintain the geographic cline across northern Oklahoma.

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Figure 1. Geographic distribution of Sceloporus undulatus subspecies in Oklahoma (From Webb, 1970). Areas of intergradation are shaded.

(1) Eastern Plateau Lizard, S. u. erythrocheilus,

(2) Northern Prairie Lizard, S. u. garmani,

(3) Southern Prairie Lizard, S. u. consobrinus,

(4) Northern Fence Lizard, S. u. hyacinthinus.

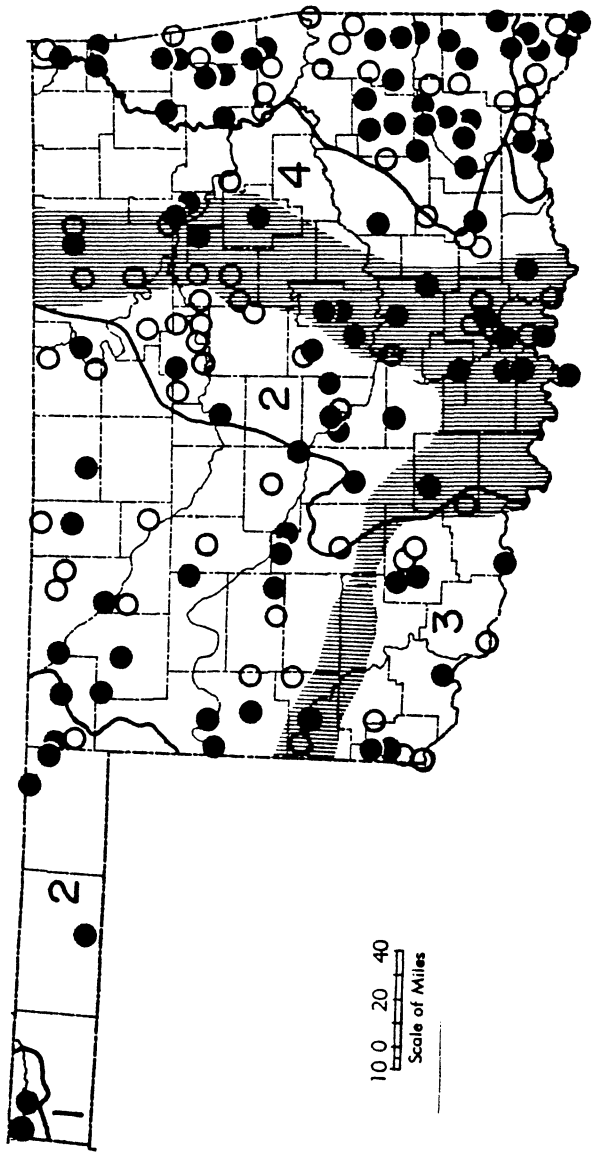

4
2
3
2
1
10 0 20 40
Scale of Miles

Figure 2. Sceloporus undulatus garmani

Figure 3. Sceloporus undulatus hyacinthinus

Figure 4. Locations of collection sites along the Cimarron River.

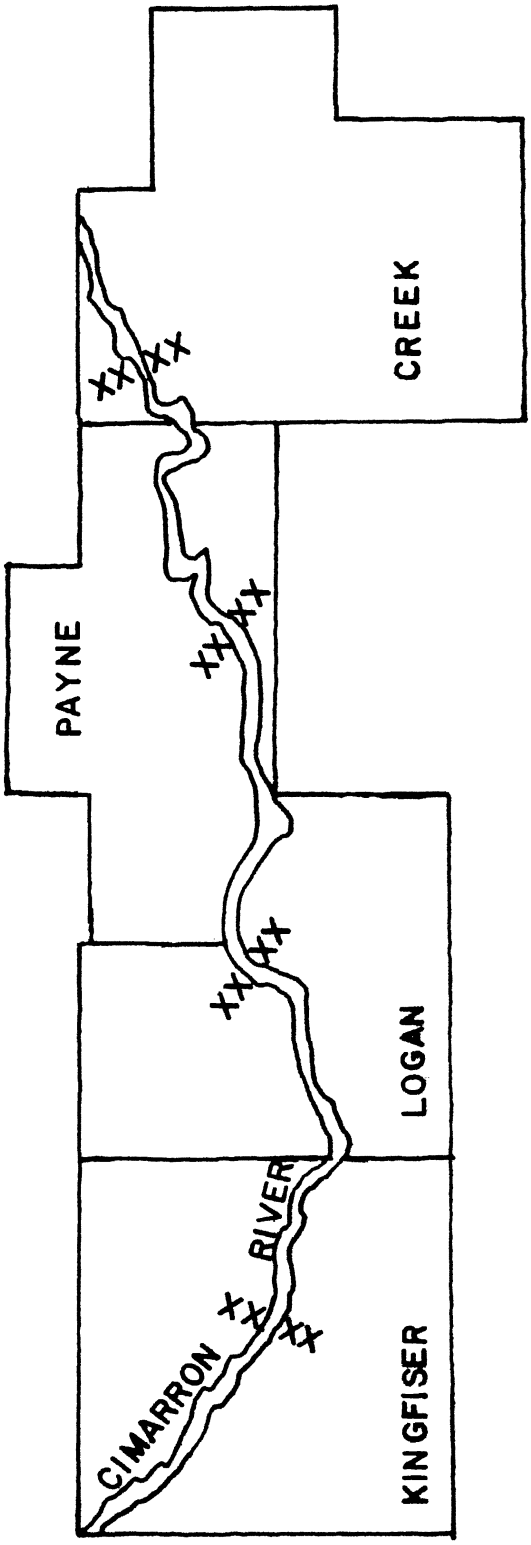

CREEK
PAYNE
LOGAN
KINGFISER
CIMARRON RIVER

Figure 5. Sampling design for sites at each county.

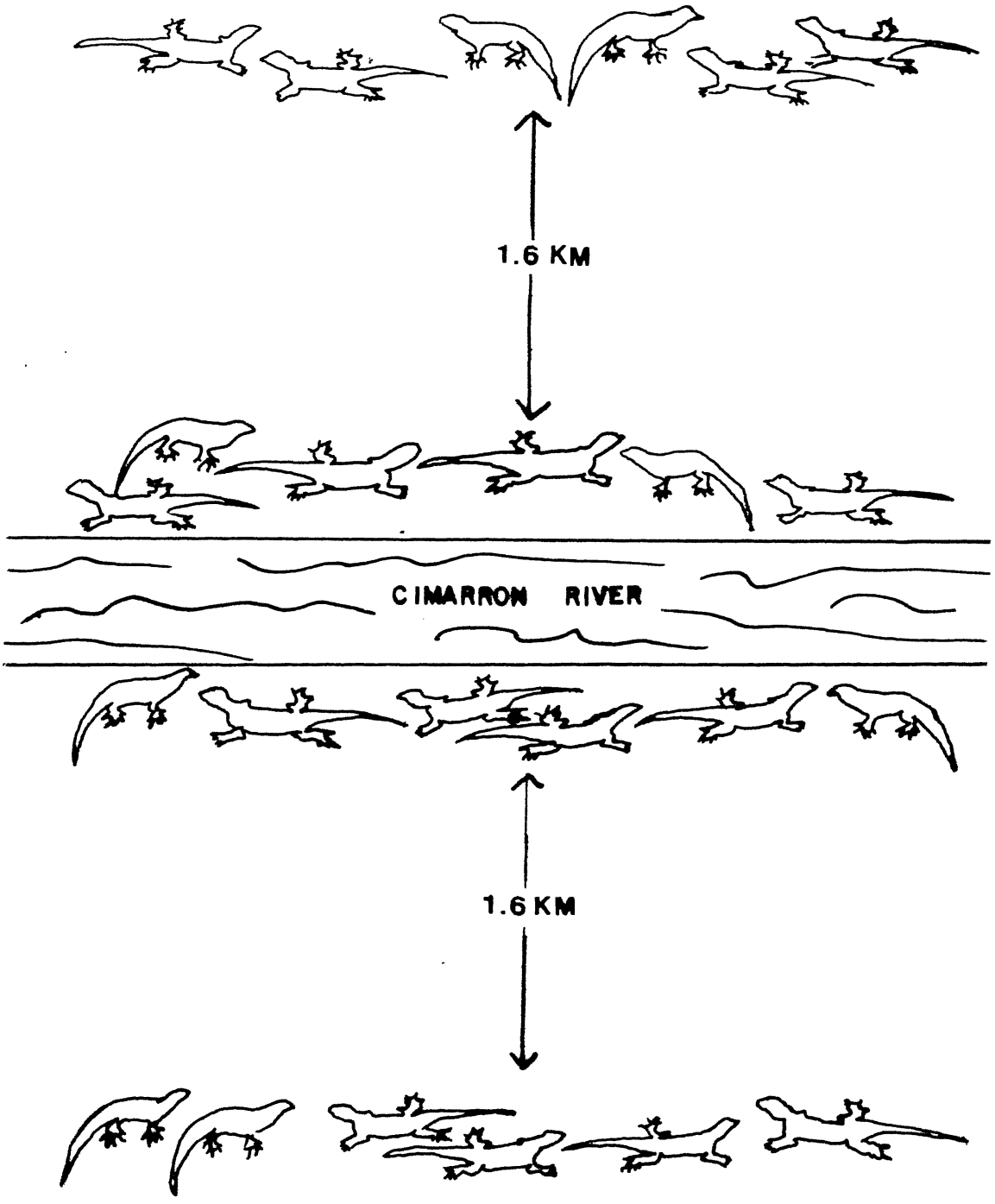

1.6 KM
CIMARRON RIVER
1.6 KM

Figure 6. Geographic pattern of allelic frequencies for LDH-2. Site designations as in Table I.

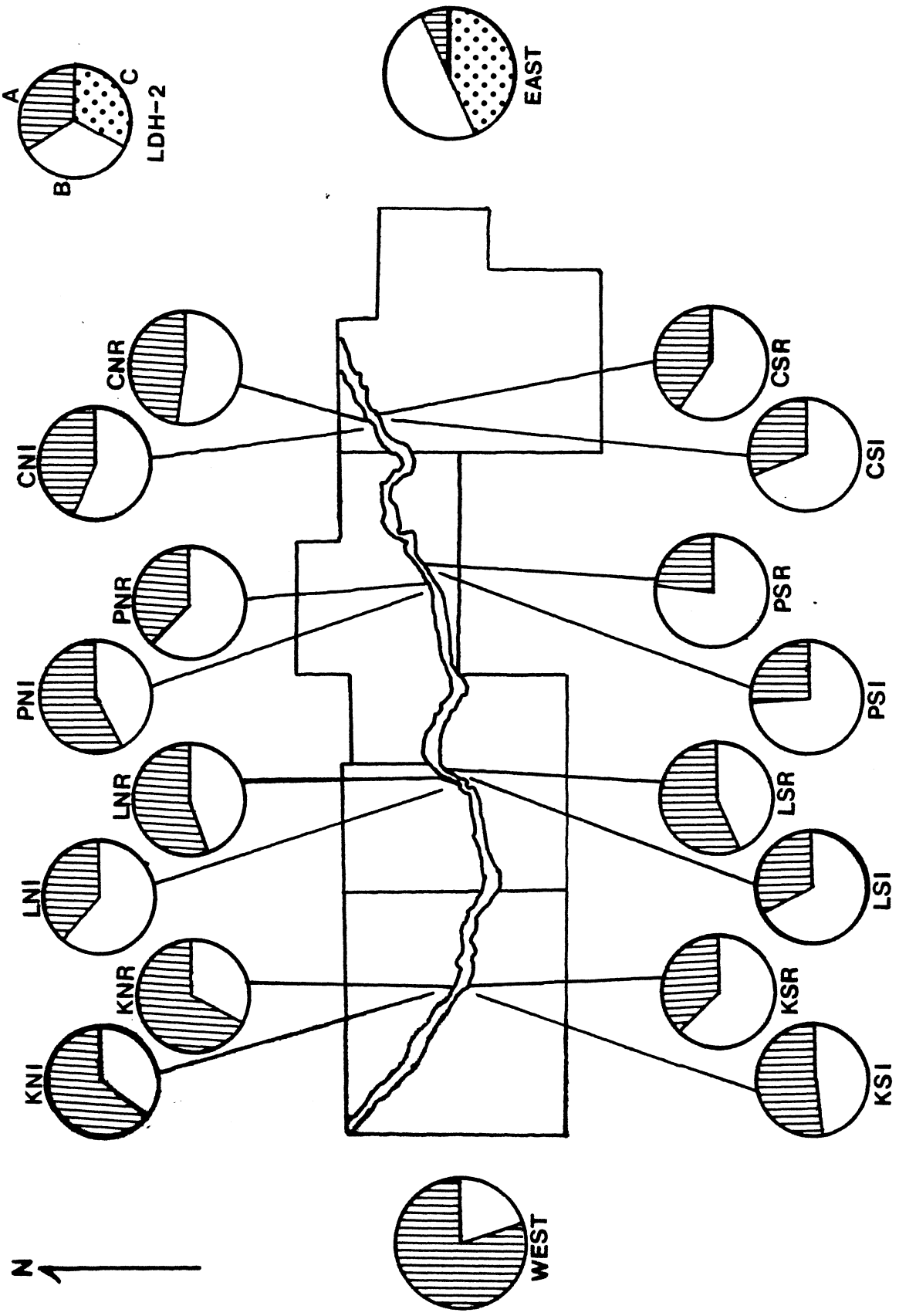

A
B
C
LDH-2
EAST
CNR
CNI
CSR
CSI
PNR
PNI
PSR
PSI
LNR
LNI
LSR
LSI
KNR
KNI
KSR
KSI
WEST
N

Figure 7. Geographic pattern of allelic frequencies for PGM. Site designations as in Table I.

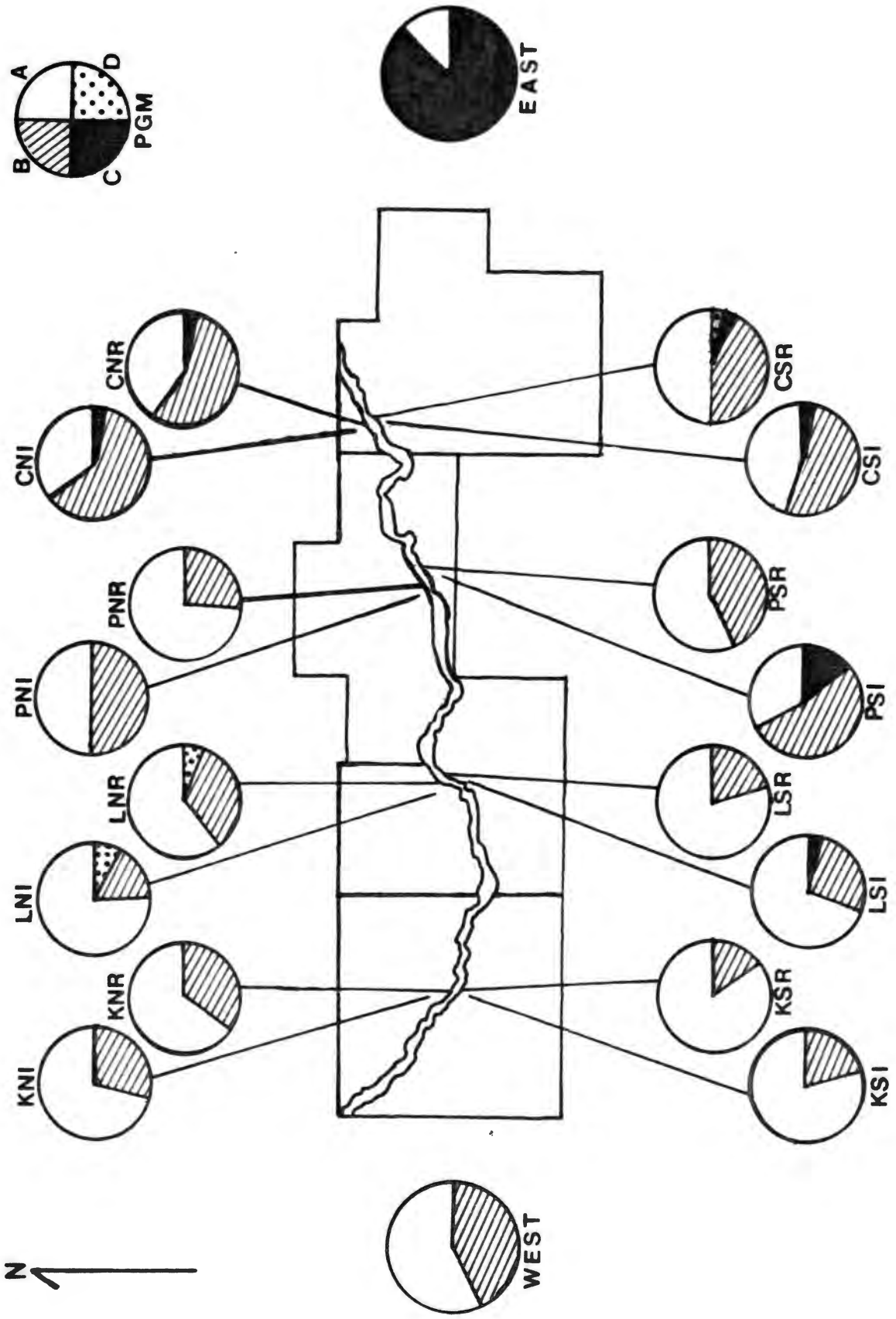

A
B
C
D
PGM
EAST
WEST
N
CNR
CNI
PNR
PNI
LNR
LNI
KNR
KNI
CSR
CSI
PSR
PSI
LSR
LSI
KSR
KSI

Figure 8. Geographic pattern of allelic frequencies for MPI. Site designations as in Table I.

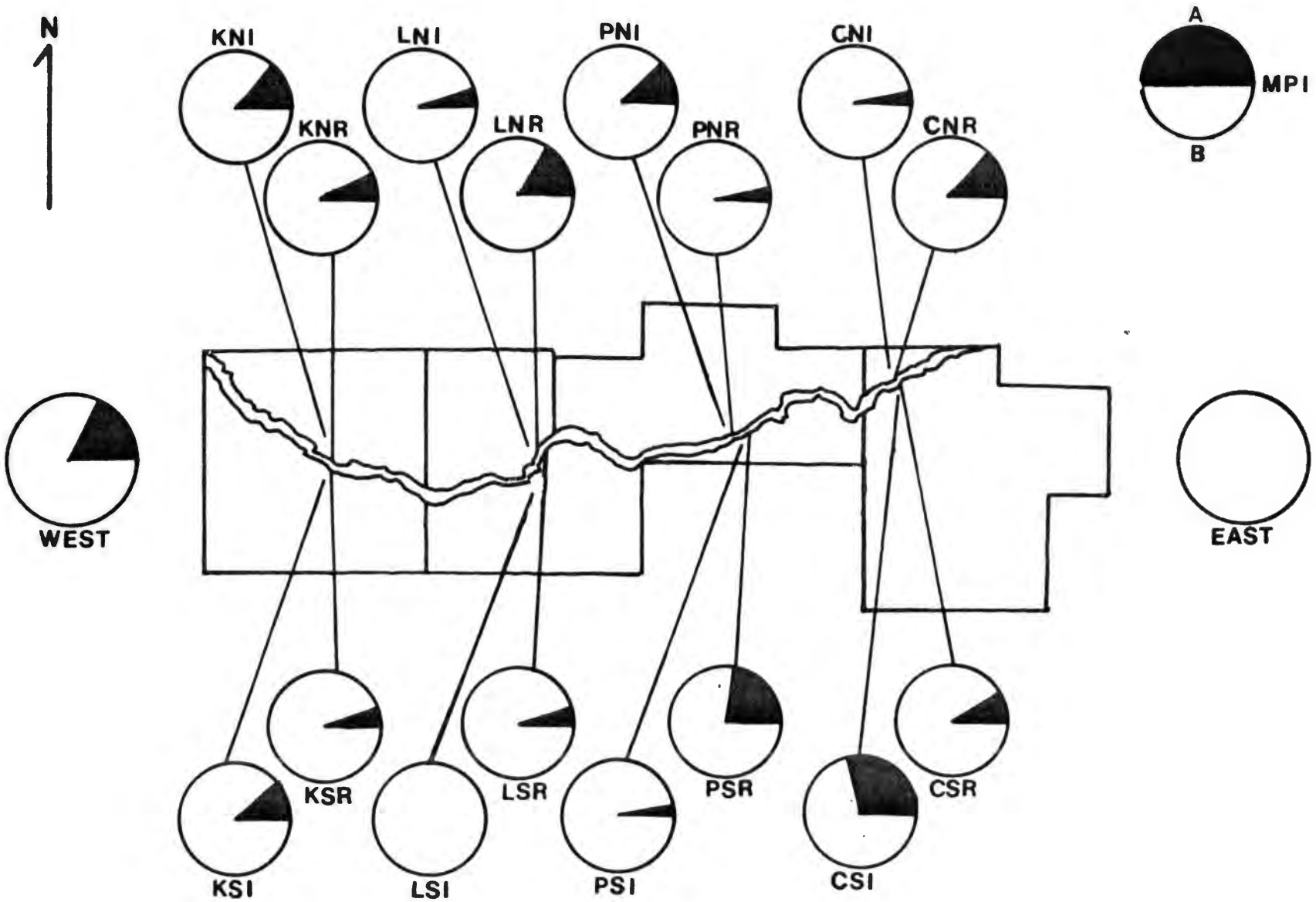

N
KNI
KNR
LNI
LNR
PNI
PNR
CNI
CNR
A
MPI
B
WEST
EAST
KSI
KSR
LSI
LSR
PSI
PSR
CSI
CSR

Figure 9. Fst values for various subdivisions of all samples along the Cimarron River.

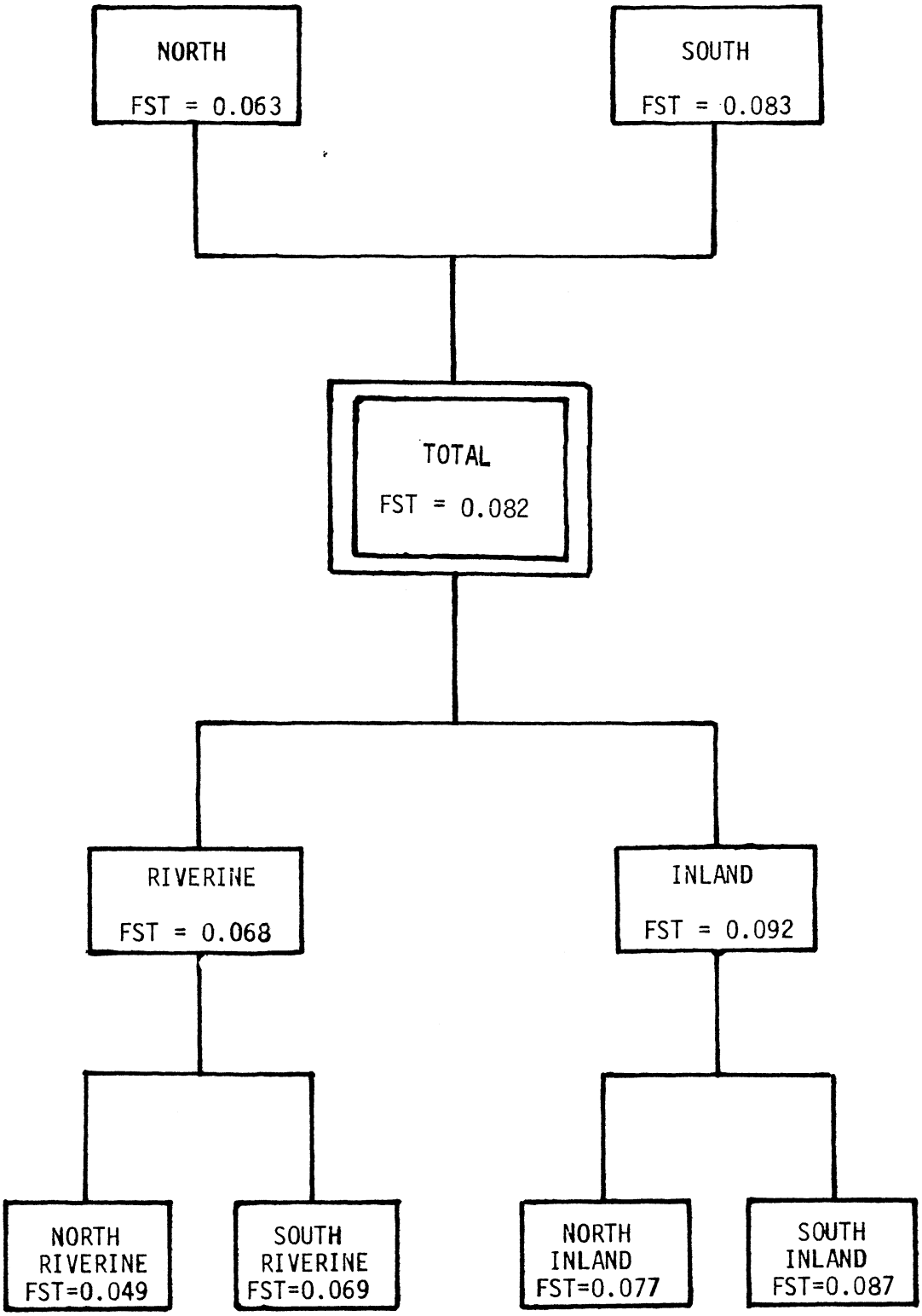

NORTH
FST = 0.063
SOUTH
FST = 0.083
TOTAL
FST = 0.082
RIVERINE
FST = 0.068
INLAND
FST = 0.092
NORTH RIVERINE FST=0.049
SOUTH RIVERINE FST=0.069
NORTH INLAND FST=0.077
SOUTH INLAND FST=0.087

Figure 10. Homogeneity among populations for PGM. Black circles and white circles each represent separate homogeneous groups. Two-toned circles represent samples which were members of both groups. Population designations as in Table I.

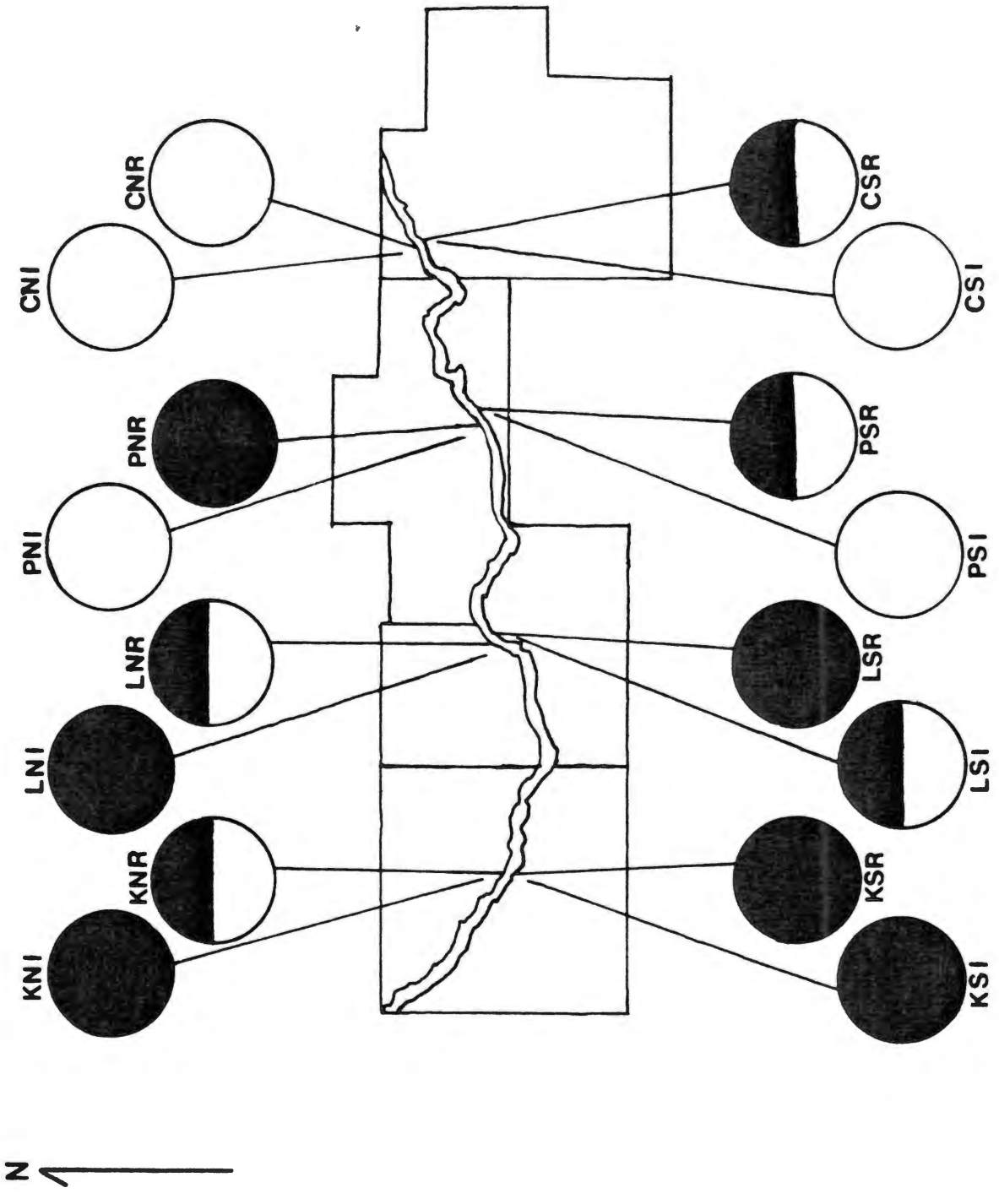

CNR
CNI
CSR
CSI
PNR
PNI
PSR
PSI
LNR
LNI
LSR
LSI
KNR
KNI
KSR
KSI
N

Figure 11. Homogeneity among populations for LDH-2. Black circles and white circles each represent separate homogeneous groups. Two-toned circles represent samples which were members of both groups. Population designations as in Table I.

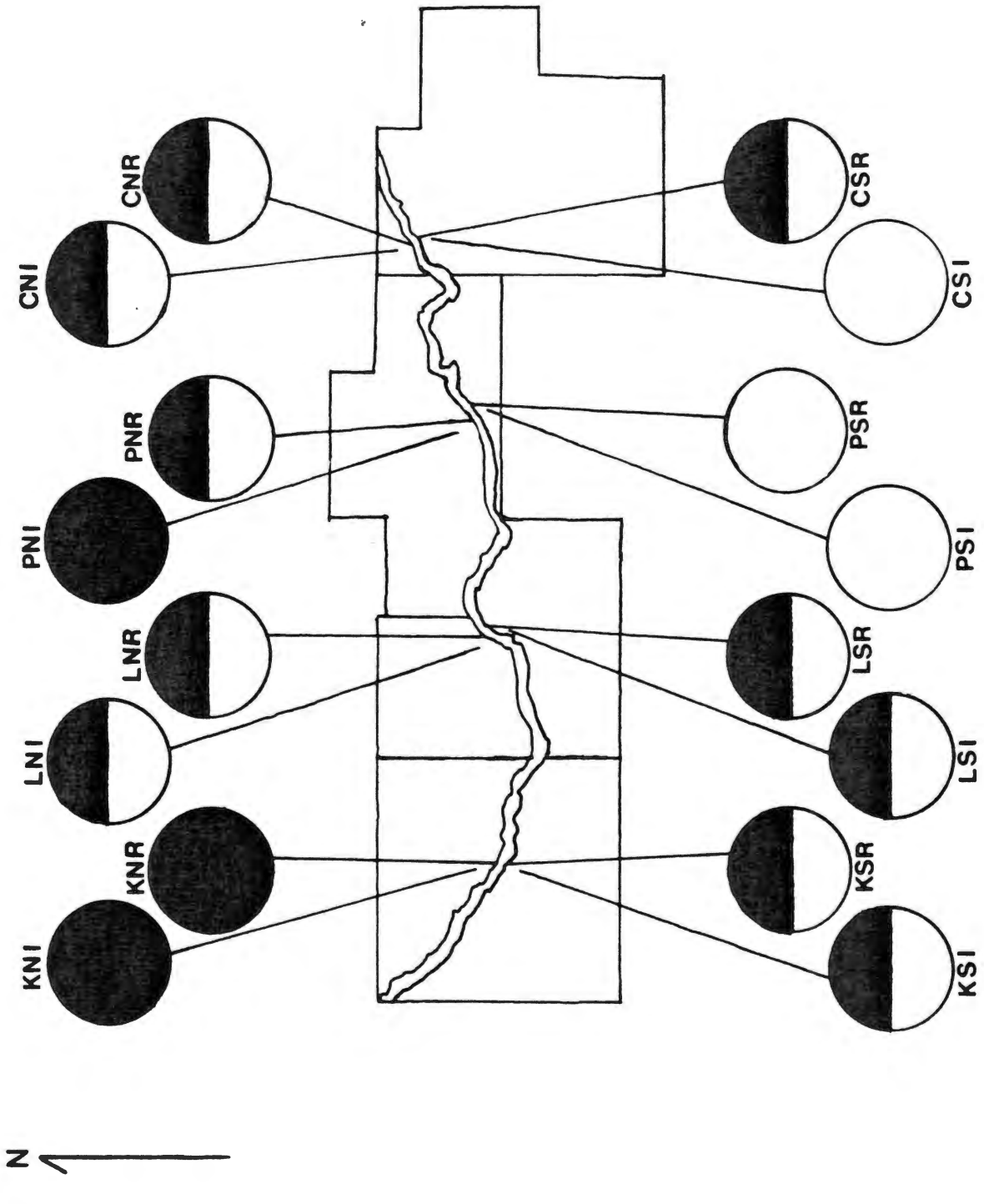

CNR
CNI
PNR
PNI
LNR
LNI
KNR
KNI
CSR
CSI
PSR
PSI
LSR
LSI
KSR
KSI
N

Figure 12. Homogeneity among populations for MPI. Black circles and white circles each represent separate homogeneous groups. Two-toned circles represent samples which were members of both groups. Population designations as in Table I.

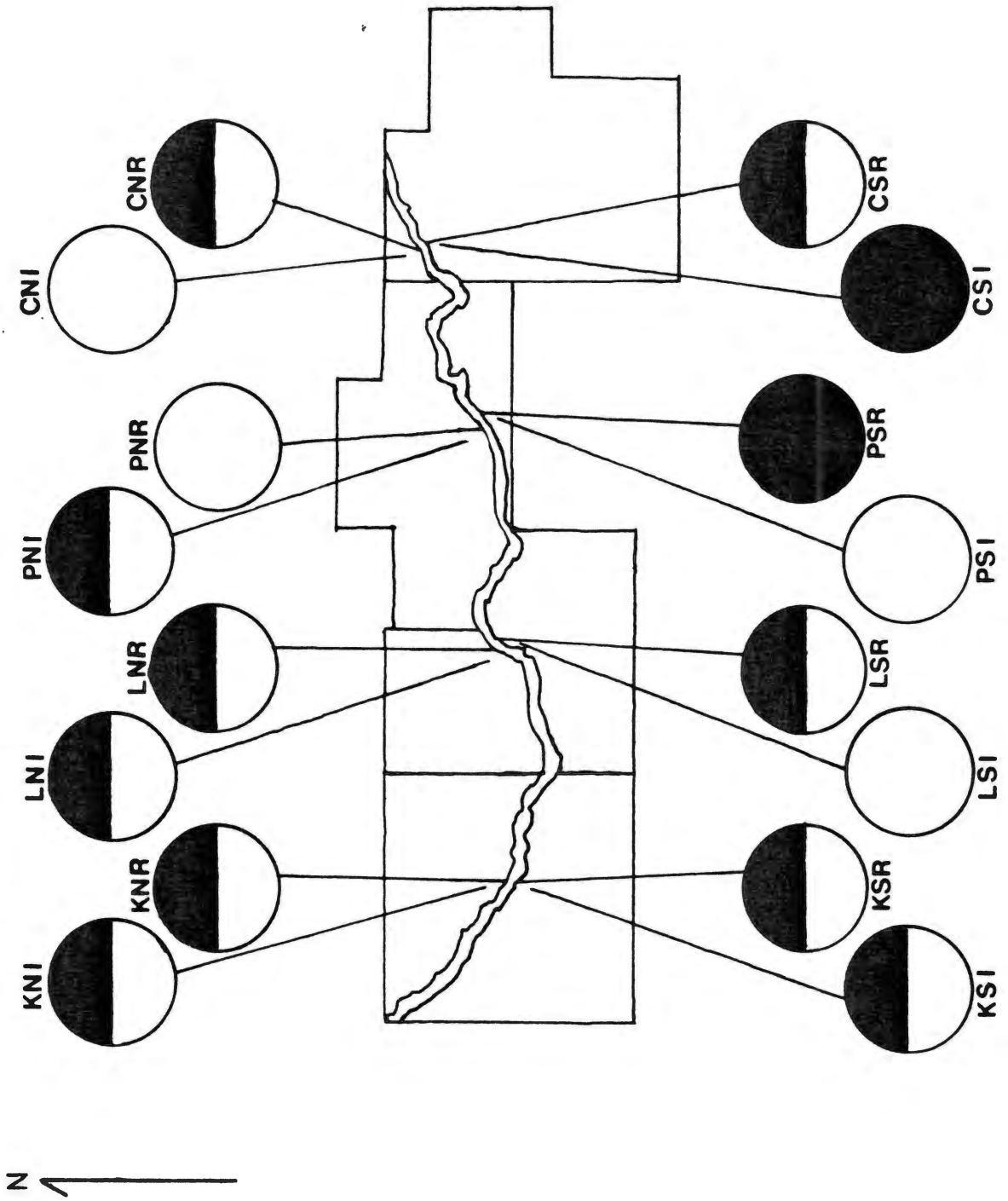

CNR
CNI
CSR
CSI
PNR
PNI
PSR
PSI
LNR
LNI
LSR
LSI
KNR
KNI
KSR
KSI
N

Figure 13. Distribution of S. undulatus populations on the first two principal component axes. All populations except the far east population from Cherokee Co., OK (East) and the far west population from Woods Co., OK (West) are designated by a three letter sequence in which the first letter represents the county (from west to east: Kingfisher (K), Logan (L), Payne (P) and Creek (C); the second letter specifies North (N) or South (S) of the river; and the third letter denotes Inland (I) or Riverine (R) populations.

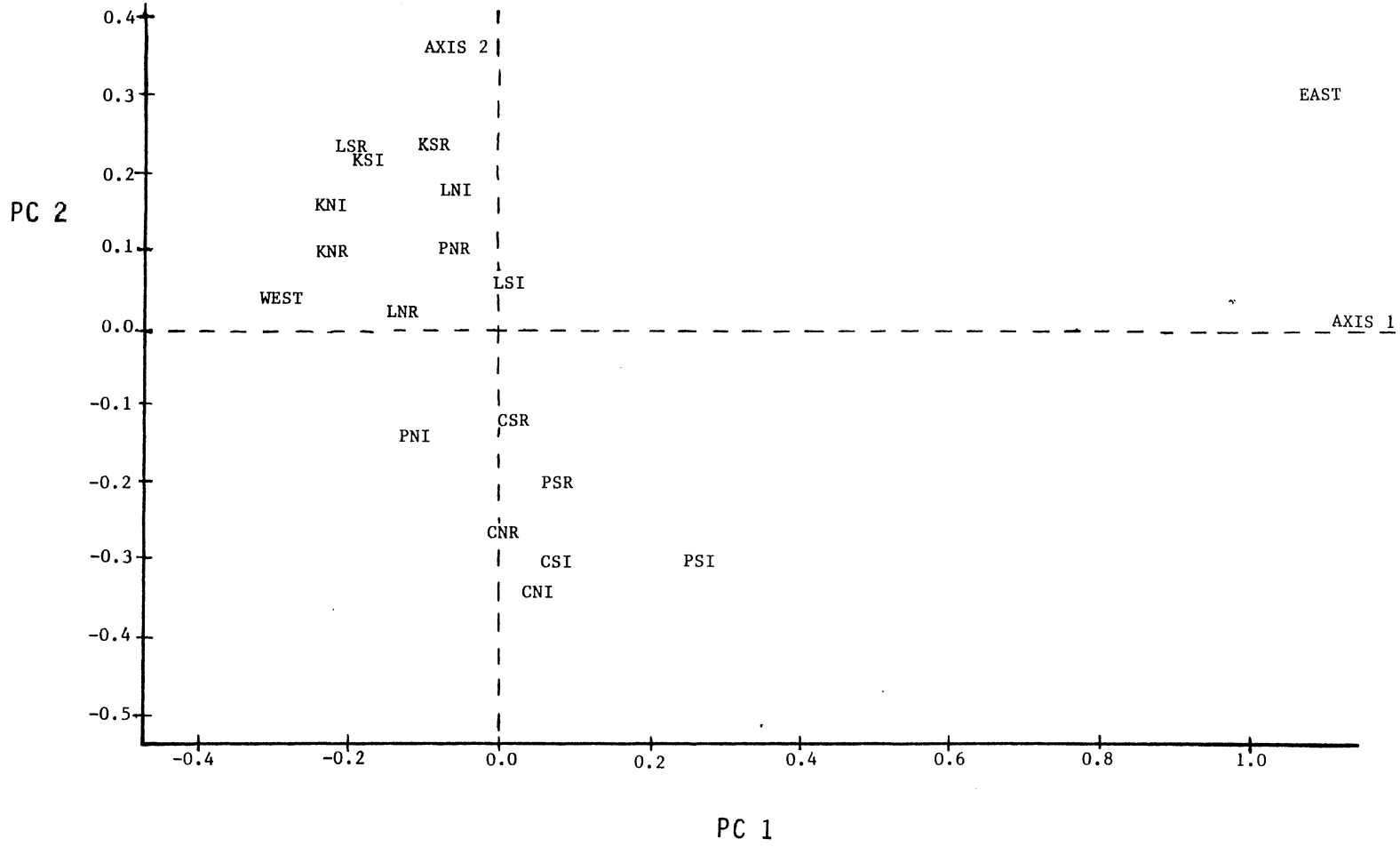

0.4
0.3
0.2
0.1
0.0
-0.1
-0.2
-0.3
-0.4
-0.5
PC 2
AXIS 2
AXIS 1
EAST
LSR
KSR
KSI
LNI
KNI
KNR
PNR
LSI
WEST
LNR
CSR
PNI
PSR
CNR
CSI
PSI
CNI
-0.4
-0.2
0.0
0.2
0.4
0.6
0.8
1.0
PC 1

Figure 14. Cluster analysis of genetic distances using the unweighted pair-group method (Sneath and Sokal 1973). Population designations as in Table I.

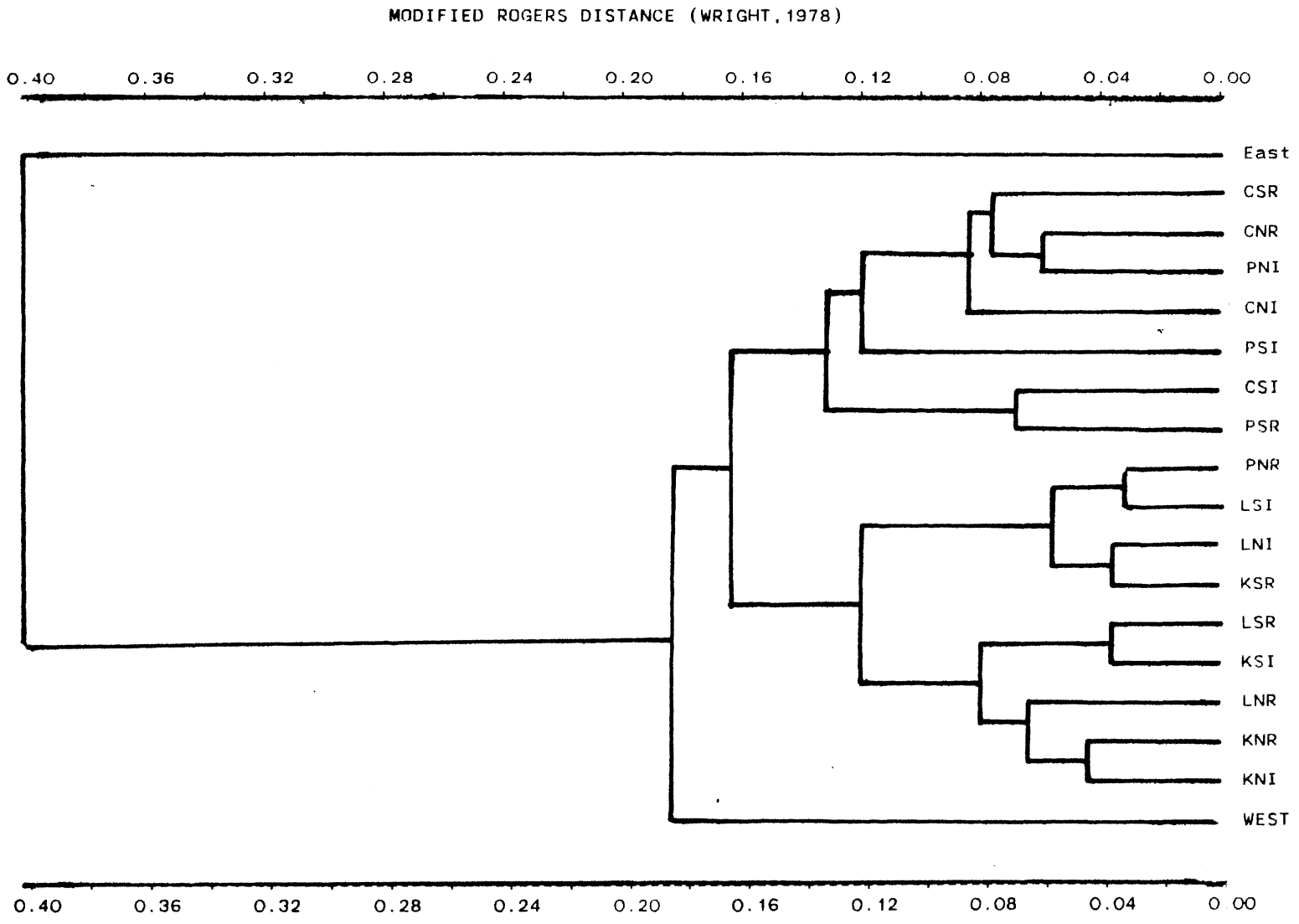
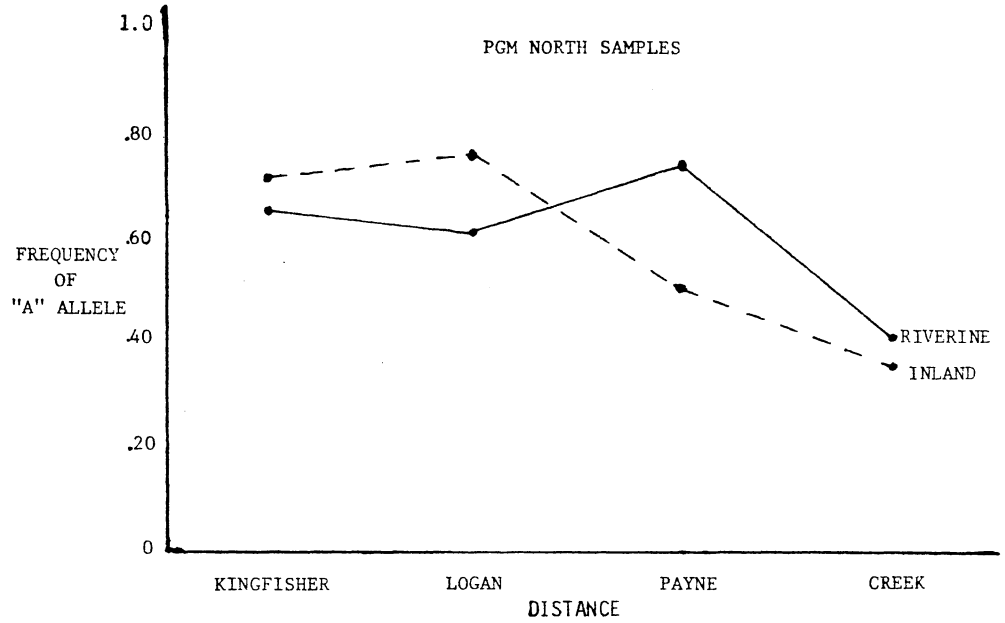

MODIFIED ROGERS DISTANCE (WRIGHT, 1978)
0.40
0.36
0.32
0.28
0.24
0.20
0.16
0.12
0.08
0.04
0.00
East
CSR
CNR
PNI
CNI
PSI
CSI
PSR
PNR
LSI
LNI
KSR
LSR
KSI
LNR
KNR
KNI
WEST
0.40
0.36
0.32
0.28
0.24
0.20
0.16
0.12
0.08
0.04
0 00

Figure 15. Clinal pattern of PGM-A (counties from west to east Kingfisher, Logan, Payne, and Creek).


PGM NORTH SAMPLES
1.0
.80
.60
.40
.20
0
FREQUENCY OF "A" ALLELE
RIVERINE
INLAND
KINGFISHER
LOGAN
PAYNE
CREEK
DISTANCE

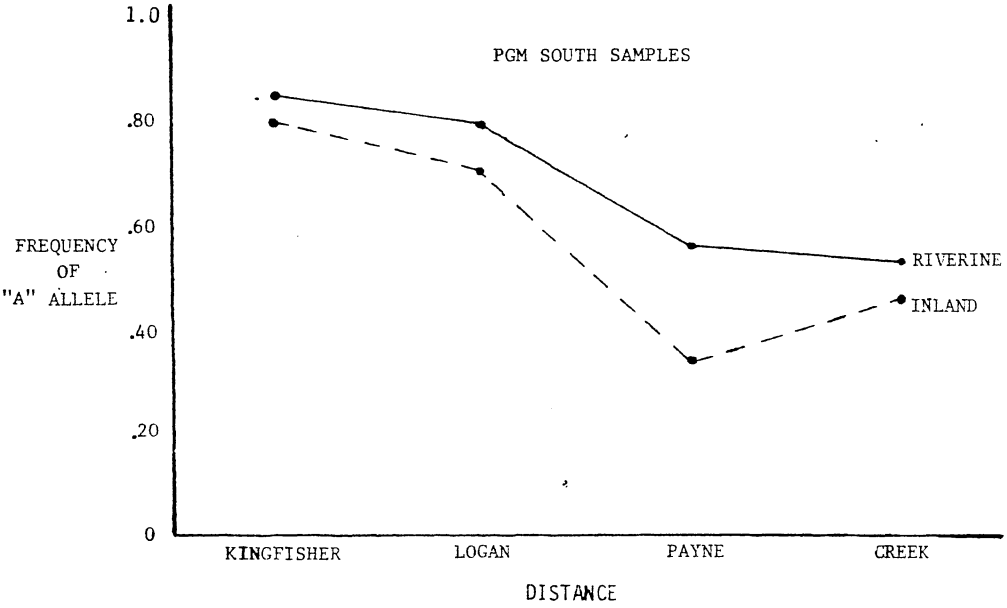
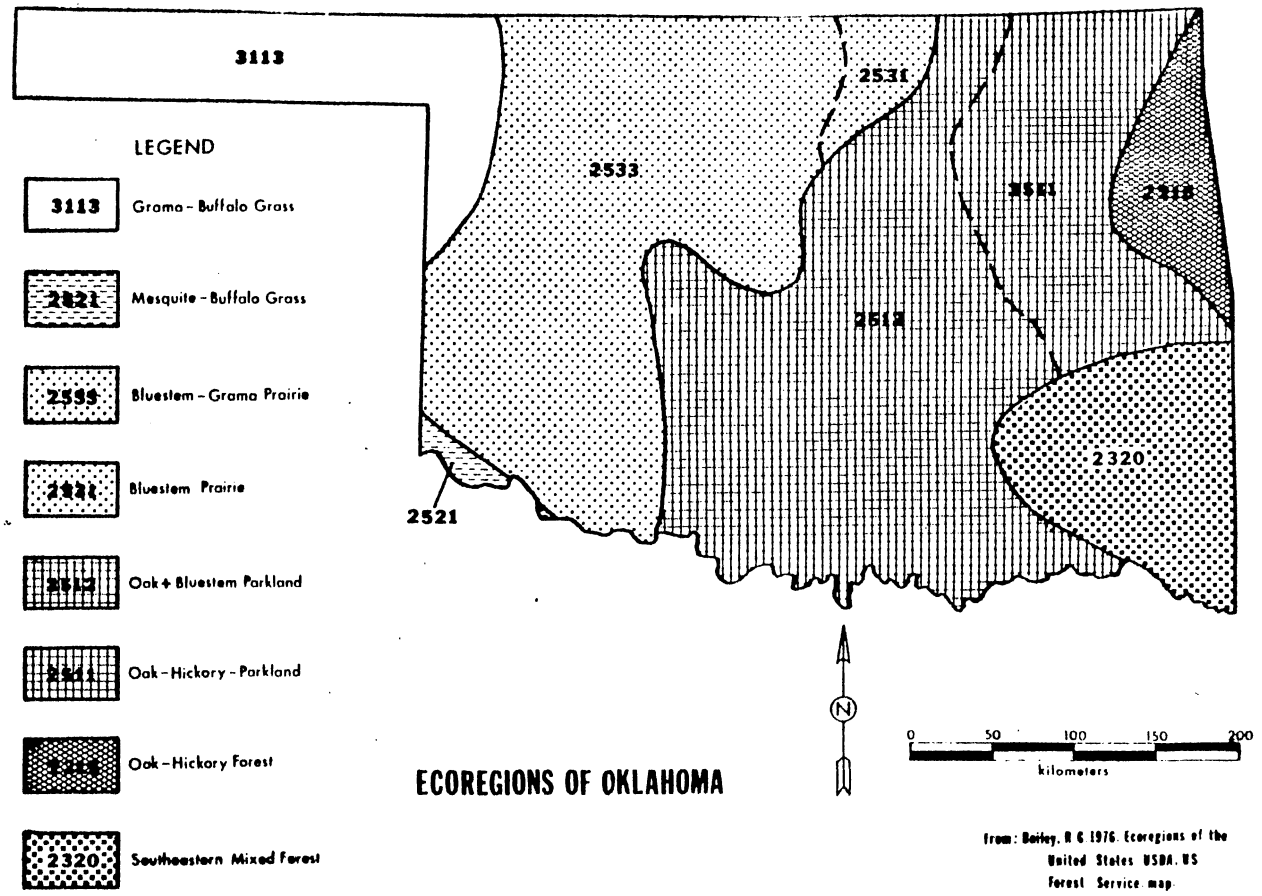

PGM SOUTH SAMPLES
1.0
.80
.60
.40
.20
0
FREQUENCY OF "A" ALLELE
RIVERINE
INLAND
KINGFISHER
LOGAN
PAYNE
CREEK
DISTANCE

Figure 16. Ecoregions of Oklahoma (From Bailey 1976).



ECOREGIONS OF OKLAHOMA

from: Bailey, R G 1976. Ecoregions of the United States USDA, US Forest Service map.

TABLE I

ALLELIC FREQUENCIES IN ALL POPULATIONS*

LOCUS	EAST	CSR	CSI	CNR	CNI	PSR	PSI	PNR	PNI	LSR	LSI	LNR	LNI	KSR	KSI	KNR	KNI	WEST
LDH-1																		
(N)	16	22	21	21	23	22	21	21	20	22	20	19	21	20	22	20	21	20
A	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
LDH-2																		
(N)	16	22	21	21	23	22	21	21	20	22	20	19	21	20	22	20	21	20
A	0.063	0.409	0.310	0.476	0.435	0.227	0.262	0.381	0.575	0.568	0.325	0.553	0.381	0.375	0.523	0.675	0.643	0.800
B	0.500	0.591	0.690	0.524	0.565	0.773	0.738	0.619	0.425	0.432	0.675	0.447	0.619	0.625	0.477	0.325	0.357	0.200
C	0.438	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
MDH-1																		
(N)	16	22	21	21	23	22	21	21	20	22	20	19	21	20	22	20	21	20
A	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
MDH-2																		
(N)	16	22	21	21	23	22	21	21	20	22	20	19	21	20	22	20	21	20
A	0.000	0.023	0.048	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.075
B	1.000	0.977	0.952	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.925
PGM																		
(N)	16	22	21	21	23	22	21	21	20	22	20	19	21	20	22	20	21	20
A	0.125	0.523	0.452	0.405	0.348	0.568	0.333	0.738	0.500	0.795	0.700	0.605	0.762	0.850	0.795	0.650	0.714	0.575
B	0.000	0.432	0.524	0.571	0.630	0.432	0.524	0.262	0.500	0.205	0.275	0.342	0.167	0.150	0.205	0.350	0.286	0.425
C	0.875	0.023	0.024	0.024	0.022	0.000	0.143	0.000	0.000	0.000	0.025	0.000	0.000	0.000	0.000	0.000	0.000	0.000
D	0.000	0.023	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.053	0.071	0.000	0.000	0.000	0.000	0.000
MPI																		
(N)	16	22	21	21	23	22	21	21	20	22	20	19	21	20	22	20	21	20
A	0.000	0.091	0.286	0.143	0.022	0.227	0.024	0.024	0.125	0.045	0.000	0.158	0.048	0.050	0.114	0.075	0.143	0.175
B	1.000	0.909	0.714	0.857	0.978	0.773	0.976	0.976	0.875	0.955	1.000	0.842	0.952	0.950	0.886	0.925	0.857	0.825
GOT																		
(N)	16	22	21	21	23	22	21	21	20	22	20	19	21	20	22	20	21	20
A	0.000	0.000	0.000	0.000	0.000	0.023	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
B	1.000	1.000	1.000	1.000	1.000	0.977	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000

*All populations except the far east population from Cherokee Co., OK (East) and the far west population from Woods Co., OK (West) are designated by a three letter sequence in which the first letter represents the county (from east to west: Creek (C), Payne (P), Logan (L), and Kingfisher (K)), the second letter specifies north (N) or south (S) of the river, and the third denotes inland (I) or riverine (R) populations.

TABLE II

MATRIX OF GENETIC DISTANCE (WRIGHT, 1978) ABOVE THE DIAGONAL AND MATRIX OF GENETIC SIMILARITY (NEI, 1978) BELOW THE DIAGONAL FOR ALL POPULATIONS

*POPULATION	East	CSR	CSI	CNR	CNI	PSR	PSI	PNR	PNI	LSR	LSI	LNR	LNI		KSI	KNR	KNI	WEST
East	*****	0.375	0.395	0.392	0.389	0.393	0.338	0.390	0.406	0.414	0.377	0.400	0.389	0.403	0.411	0.421	0.422	0.452
CSR	0.831	*****	0.105	0.070	0.091	0.104	0.106	0.094	0.080	0.135	0.094	0.082	0.117	0.139	0.124	0.129	0.132	0.181
CSI	0.809	0.994	*****	0.103	0.141	0.070	0.132	0.174	0.142	0.218	0.171	0.147	0.189	0.206	0.194	0.207	0.198	0.231
CNR	0.815	1.000	0.995	*****	0.063	0.136	0.119	0.159	0.059	0.180	0.162	0.104	0.183	0.204	0.171	0.141	0.153	0.166
CNI	0.821	0.996	0.983	1.000	*****	0.161	0.093	0.172	0.101	0.205	0.166	0.147	0.200	0.222	0.204	0.171	0.192	0.205
PSR	0.813	0.993	1.000	0.983	0.973	*****	0.130	0.137	0.165	0.201	0.129	0.153	0.150	0.163	0.175	0.215	0.201	0.260
PSI	0.866	0.993	0.986	0.989	0.995	0.985	*****	0.168	0.163	0.229	0.148	0.183	0.191	0.213	0.221	0.223	0.233	0.269
PNR	0.822	0.996	0.970	0.975	0.969	0.983	0.971	*****	0.145	0.088	0.031	0.110	0.040	0.051	0.079	0.139	0.129	0.215
PNI	0.801	0.999	0.982	1.000	0.994	0.972	0.973	0.981	*****	0.137	0.157	0.065	0.165	0.183	0.134	0.084	0.101	0.113
LSR	0.799	0.984	0.948	0.966	0.953	0.956	0.940	0.996	0.984	*****	0.117	0.091	0.088	0.090	0.037	0.082	0.066	0.158
LSI	0.835	0.996	0.972	0.975	0.972	0.986	0.979	1.000	0.976	0.989	*****	0.131	0.057	0.070	0.109	0.163	0.156	0.237
LNR	0.806	0.999	0.980	0.994	0.980	0.977	0.964	0.993	1.000	0.998	0.987	*****	0.118	0.136	0.080	0.070	0.059	0.120
LNI	0.822	0.990	0.963	0.965	0.956	0.978	0.960	1.000	0.973	0.996	1.000	0.990	*****	0.036	0.075	0.150	0.133	0.224
KSR	0.811	0.983	0.956	0.955	0.945	0.974	0.950	1.000	0.965	0.995	0.999	0.985	1.000	*****	0.076	0.162	0.141	0.236
KSI	0.799	0.987	0.959	0.969	0.953	0.968	0.944	0.998	0.984	1.000	0.991	1.000	0.999	0.999	*****	0.096	0.066	0.164
KNR	0.789	0.986	0.952	0.982	0.969	0.947	0.943	0.982	0.999	0.998	0.973	1.000	0.978	0.974	0.995	*****	0.044	0.086
KNI	0.786	0.984	0.956	0.977	0.959	0.954	0.937	0.986	0.994	1.000	0.976	1.000	0.984	0.982	1.000	.000	*****	0.101
WEST	0.750	0.964	0.936	0.972	0.953	0.918	0.913	0.949	0.991	0.976	0.936	0.989	0.943	0.938	0.973	0.998	0.995	*****

*Population designation as in Table I.

TABLE III

MODIFIED ROGER'S GENETIC DISTANCES (WRIGHT, 1978) BETWEEN ALL PAIRS OF POPULATIONS IN WHICH LIKE PAIRS (NORTH - NORTH AND SOUTH - SOUTH) FALL ABOVE THE DIAGONAL AND UNLIKE PAIRS (NORTH - SOUTH) FALL BELOW THE DIAGONAL

* Population	CSR	CSI	CNR	CNI	PSR	PSI	PNR	PNI	LSR	LSI	LNR	LNI	KSR	KSI	KNR	KNI
CSR	-----	0.105			0.104	0.106			0.135	0.094			0.139	0.124		
CSI		-----			0.070	0.132			0.218	0.171			0.206	0.194		
CNR	0.070	0.103	-----	0.063			0.159	0.059			0.104	0.183			0141	0.153
CNI	0.091	0.141		-----			0.172	0.101			0.147	0.200			0.171	0.192
PSR			0.136	0.161	-----	0.130			0.210	0.129			0.163	0.175		
PSI			0.119	0.093		-----			0.229	0.148			0.213	0.221		
PNR	0.094	0.174			0.137	0.168	-----	0.145			0.110	0.040			0.139	0.129
PNI	0.080	0.142			0.165	0.163		-----			0.065	0.165			0.084	0.101
LSR			0.180	0.205			0.088	0.137	-----	0.117			0.090	0.037		
LSI			0.162	0.166			0.031	0.157		-----			0.070	0.109		
LNR	0.082	0.147			0.153	0.183			0.091	0.131	-----	0.118			0.070	0.059
LNI	0.117	0.189			0.150	0.191			0.088	0.057		-----			0.150	0.133
KSR			0.204	0.222			0.051	0.183			0.136	0.036	-----	0.076		
KSI			0.171	0.204			0.079	0.134			0.080	0.075		-----		
KNR	0.129	0.207			0.215	0.223			0.082	0.163			0.162	0.096	-----	0.044
KNI	0.132	0.198			0.201	0.233			0.066	0.156			0.141	0.066		-----

*Population designations as in Table I.

TABLE IV

CHI-SQUARE TEST COMPARING GENOTYPES FROM AREAS NORTH AND SOUTH OF THE RIVER IN KINGFISHER CO. FOR LDH

	AA	AB	BB	TOTAL
SOUTH				
OBSERVED	17	20	4	41
EXPECTED	13.8	17.8	9.4	
NORTH				
OBSERVED	11	16	15	42
EXPECTED	14.2	18.2	9.6	
TOTAL	28	36	19	83

Chi-square value = 8.088 df = 2 $p < 0.02$

TABLE V

CHI-SQUARE TEST COMPARING GENOTYPES FROM AREAS NORTH AND SOUTH OF THE RIVER IN PAYNE CO. FOR LDH

	AB	AA	BB	TOTAL
SOUTH				
OBSERVED	17	11	13	41
EXPECTED	18.5	5.4	17.1	
NORTH				
OBSERVED	21	0	22	43
EXPECTED	19.5	5.6	17.9	
TOTAL	38	11	35	84

Chi-square value = 13.695 df = 2 $p < 0.01$

TABLE VI

CHI-SQUARE TEST COMPARING GENOTYPES FROM AREAS NORTH AND SOUTH OF THE RIVER FOR MPI IN LOGAN COUNTY

	BB	AB	TOTAL
SOUTH			
OBSERVED	31	9	40
EXPECTED	34.6	5.4	
NORTH			
OBSERVED	40	2	42
EXPECTED	36.4	5.6	
TOTAL	71	11	82

Chi-square value = 5.550 df = 1 $p < 0.02$

TABLE VII

CHI-SQUARE TEST COMPARING GENOTYPES FROM AREAS NORTH AND SOUTH OF THE RIVER FOR MPI IN CREEK COUNTY

	BB	AB	AA	TOTAL
SOUTH				
OBSERVED	38	5	1	44
EXPECTED	32.9	10.6	0.5	
NORTH				
OBSERVED	27	16	0.0	43
EXPECTED	32.1	10.4	0.5	
TOTAL	65	21	1	87

Chi-square value = 8.613 df = 2 $p < 0.02$

TABLE VIII

CHI-SQUARE TEST COMPARING GENOTYPES FROM AREAS NORTH AND SOUTH OF THE RIVER IN CREEK COUNTY FOR PGM

	AA	AB	BB	TOTAL
SOUTH				
OBSERVED	8	26	9	43
EXPECTED	8.4	20.3	14.3	
NORTH				
OBSERVED	9	15	20	44
EXPECTED	8.6	20.7	14.7	
TOTAL	17	41	29	87

Chi-square value = 7.172 df = 2 $p < 0.03$

TABLE IX

PRINCIPAL COMPONENT LOADINGS

Variables	Axis 1	Axis 2	Axis 3	Axis 4
LDH-1	0	0	0	0
MDH-2	0	0	0	0
LDH-2-A	-0.809	0.135	-0.571	0.035
LDH-2-B	0.346	-0.392	0.852	0.008
LDH-2-C	0.893	0.344	-0.263	-0.072
MDH-2	0.167	0.185	0.374	0.424
PGM-A	-0.743	0.530	0.405	-0.025
PGM-B	-0.271	-0.940	-0.476	0.050
PGM-C	0.9355	0.257	-0.240	-0.013
PGM-D	-0.1.2	0.000	0.173	-0.040
MPI	0.300	0.377	0.135	0.865
GOT	-0.066	0.234	-0.343	0.436
% of variance	51.1	24.7	20.8	2.9
Cumulative % of variance	51.1	75.8	96.6	99.5

TABLE X

MODIFIED ROGER'S GENETIC DISTANNCES (WRIGHT, 1978) BETWEEN PAIRS OF POPULATIONS IN WHICH LIKE RIVERINE PAIRS (NORTH - NORTH AND SOUTH - SOUTH) FALL BELOW THE DIAGONAL AND LIKE INLAND PAIRS (NORTH - NORTH AND SOUTH - SOUTH) FALL ABOVE THE DIAGONAL

*Population	CSR	CSI	CNR	CNI	PSR	PSI	PNR	PNI	LSR	LSI	LNR	LNI	KSR	KSI	KNR	KNI
CSR	-----															
CSI		-----				0.132				0.171				0.194		
CNR			-----													
CNI				-----				0.101				0.200				0.192
PSR	0.104				-----											
PSI						-----				0.148				0.221		
PNR			0.159				-----									
PNI								-----				0.165				0.101
LSR	0.135				0.201				-----							
LSI										-----				0.109		
LNR			0.104				0.110				-----					
LNI												-----				0.133
KSR	0.139				0.163				0.090				-----			
KSI														-----		
KNR			0.141				0.139				0.070				-----	
KNI																-----

*Population designations as in Table I.

TABLE XI

CHI-SQUARE TESTS COMPARING GENOTYPES OF JUVENILES TO ADULTS

COUNTY	ENZYME	*CHI-SQUARE VALUE	DF	NUMBER OF ADULTS	NUMBER OF JUVENILES
CREEK	PGM	0.815	2	32	55
	MPI	1.883	2	32	55
	LDH-2	0.101	2	32	55
KING-FISHER	PGM	0.210	2	47	36
	MPI	1.980	2	47	36
	LDH-2	0.453	2	47	36
LOGAN	PGM	1.470	2	40	42
	MPI	0.784	1	40	42
	LDH-2	1.614	2	40	42
PAYNE	PGM	3.086	2	25	59
	MPI	2.554	2	25	59
	LDH-2	2.014	2	25	59

* ALL TESTS INSIGNIFICANT = 0.05

TABLE XII

CHI-SQUARE TEST COMPARING HATCHLINGS TO ADULTS FOR MPI IN KINGFISHER COUNTY

	BB	AB	AA	TOTAL
ADULTS	63 59.0	8 12.1	1 0.9	72
HATCHLINGS	5 9.0	6 1.9	0 0.1	11
TOTAL	68	14	1	83

Chi-square value = 12.884 df = 2 $p < 0.01$

TABLE XIII

CHI-SQUARE TEST COMPARING HATCHLINGS TO ADULTS FOR PGM IN PAYNE COUNTY

	AA	AB	BB	TOTAL
ADULTS	24	26	10	60
HATCHLINGS	2 7.4	12 10.9	10 5.7	24
TOTAL	26	38	20	84

Chi-square value = 10.222 df = 2 $p < 0.01$

APPENDIX A

ELECTROPHORETIC TECHNIQUES

A lithium hydroxide buffer system was used to assay PGM, MPI, and GOT while MDH and LDH were assayed by the use of a Tris-citrate (pH = 6.0) buffer system. Distilled water was used in all buffers and stains.

Buffer Systems

LIOH tray buffer (8 liters)

10.08 g LIOH water
add 8 liters water
gradually mix in 94.0 g boric acid
pH to 8.3 with HCl

Use full strength in electrode trays.

LIOH gel buffer (2 liters)

Mix 60.5 g Tris with
16.8 g citric acid
add water to 2 liters

pH to 8.3.

For each gel mix together
25 ml tray buuffer
50 ml gel buffer
175 ml water
30 g starch
Heat slowly to 80 C
evacuate 1.5 mins.
Pour immediately into gel tray
oiled with mineral oil.

Run at 400 volts (2.5-5.0 hrs.)

Tris-citrate (pH = 6.0)

Tray and Gel Buffer (6 liters)

Mix 162 g Tris with
*96-108.6 g citric acid
bring to 6 liters with water.
pH to 6.0

Use full strength for electrode trays.

For each gel mix
8.8 ml buffer
add water to 250 ml
30 gm starch
Heat slowly to 80 C

evacuate 1.5 mins.

Pour immediately into gel tray
oiled with mineral oil.

Run at 200 volts (2.5-3 hrs).

Setting up gels

Use Whatman # 2 filter paper to make tabs 2-3mm by 7mm. Make a strait cut across the middle of the gel in which to place samples. For each sample, handle tabs with clean tweezers and saturate with tissue homogenate, place tabs in gel 3-4 mm. apart. Rinse tweezers between specimens. When all tabs are in place, push gel pieces together and use plastic wrap to hold in place. Fill electrode trays 1/2 to 2/3 full with tray buffer. Run gel 10 minutes then remove tabs.

Stains

Tray stains

MDH

35 ml distilled water

10 ml .2 M tris-HCl pH-8.0

5 ml 2 M malic acid

0.83 ml NAD (0.025 g)

0.015 g NBT (a tiny bit)

0.001 g PMS

LDH

50 ml 0.2 M tris-HCl pH-8.0

8 ml 1.0 M Lilactate (0.765 g lactic acid + 8 ml water)

0.67 ml NAD (0.02 g)

0.01 g NBT (increase this for a better stain)

0.001 g PMS (a tiny bit)

GOT

Add in the following order:

50 ml 0.2 M tris-HCl pH-8.0

a pinch Perodoxal 5 phosphate (1-2 grains)

0.07 g Aspartic acid

0.03 g a-ketoglutaric acid

0.05 g fast blue BB

Agar overlays

Agar preparation is as follows:

Heat 2% agar suspension in water in a flask in a pan of boiling water until solution is clear. For each stain, cool 12.5 ml agar to 60 C, immediately mix with the rest of the assay ingrediants, and pour over gel slice.

MPI

12.5 ml tris-HCl pH-8.0

0.02 g mannose-6-phosphate

0.1 ml of a 50 mg/ml suspension of MTT

0.1 ml of a 25 mg/ml solution of NADP

10 ul of 1000 units/ml solution of G6PD

10 ul PGI (Phosphoglucose isomerase)

0.2 mg PMS (always add last, don't expose to light)

Add to agar and incubate in dark

PGM

12.5 ml tris-HCl pH-8.0

0.06 g glucose-1-phosphate (try more if needed)

0.002 g glucose-1,6-diphosphate (a tiny bit)

0.1 ml of a 50 mg/ml suspension of MTT

0.1 ml of a 25 mg/ml solution of NADP

10 ul of 1000 units/ml solution of G6PD

MgCl off 2gm/100 ml solution

0.2 mg PMS (always add last, don't expose to light)

Add to agar and incubate in dark

APPENDIX B

VIABILITY OF EGGS EXPOSED TO CIMARRON RIVER WATER

The Cimarron River of northern Oklahoma has a high salinity content. It is possible that eggs of Sceloporus undulatus garmani may be exposed to its saline waters during floods. The purpose of this experiment was to determine whether eggs of S. u. garmani remained viable after a short exposure to Cimarron River water.

Gravid female lizards were collected in the spring of 1985 from the KSR, PSI, and LNI study sites. Females were individually housed in 18.9 liter aquaria each containing 9-14 cm of moist sand. The aquaria were checked daily for egg deposition. For each clutch, eggs were then randomly assigned to either a control group or one of 3 treatment groups. The treatment groups included exposure of eggs to Cimarron River water for 1) 1.5 hours, 2) 3 hours, or 3) 6 hours, while the control group contained only unexposed eggs. In treatment groups, eggs were totally submersed in aerated Cimarron River water so as to simulate the turbulent waters of a flood. After exposure, eggs were transferred to a plastic box filled with a mixture of 300 g of vermiculite and 240 g of distilled water. Each egg was placed 2-3 mm

below the surface of the vermiculite and the box was covered with plastic wrap to retain moisture. Eggs were maintained at 27 C in an incubator. The substrate was replaced every ten days to reduce fungal growth. Eggs were monitored for hatching, fungal growth, and deterioration.

Exposure to Cimarron River water had no effect on egg viability (Table XIV). In fact, eggs exposed to Cimarron River water seemed to leve greater viability with increaed exposure time.

In conclusion, water from the Cimarron River has no detrimental effect on the eggs of S. u. garmani and may even be beneficial. Therefore, it is feasible that eggs exposed to its waters during flooding may retain viability even after 6 hours of total submersion.

TABLE XIV

VIABILITY OF LIZARD EGGS IN DIFFERENT TREATMENT GROUPS

NUMBER EXPOSED	HOURS	PROPORTION FAILING TO HATCH	PROPORTION HATCHED
15	0.0	0.47	0.53
6	1.5	0.50	0.50
12	3.0	0.17	0.83
6	6.0	0.00	1.00

Overall viability = 0.69

VITAE

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