AN ABSTRACT OF THE THESIS OF

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Title: Genetic Variation of the Topeka Shiner, Notropis topeka, (Cypriniformes: Cyprinidae) in Kansas

Abstract Approved: [signature]

Six populations of Notropis topeka were sampled from the Arkansas River and Kansas River drainages in the Flint Hills, and one population from Wallace County in extreme western Kansas. Starch-gel electrophoresis was used to examine genic variation of N. topeka at 21 presumptive loci. Mean heterozygosity was greatest in the Arkansas River drainage ($\bar{H}$=0.048) and lowest in Wallace County ($\bar{H}$=0.015). Chi-square analysis and F-statistics indicated significant differences among populations in allele frequencies for the six most variable loci. In addition, averages of Rogers' genetic similarity values for the populations in the Arkansas River drainage were 0.946 and 0.916 for the populations in the Kansas River drainage. There was also a statistically significant correlation between Nei's genetic distance and linear geographic distance between localities. These data indicate that, while gene flow among populations is restricted or stopped, the populations are quite similar and the restriction in gene flow must be recent.

GENETIC VARIATION OF THE TOPEKA SHINER, *Notropis topeka*, (Cypriniformes: Cyprinidae) IN KANSAS

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Approved by Major Advisor

Approved by Committee Member

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This thesis is dedicated to my parents, Jim and Joan,

my grandmother, Loretta,

and my wife, Rachelle

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INTRODUCTION

Electrophoretic analyses of a wide variety of vertebrate taxa have demonstrated that the distribution of available genetic resources is not continuous over small geographic and ecological distances (Selander, 1970; Ryman et al., 1979; Chesser, 1983; Brown, 1986) or large distances (Ryman et al., 1980; Graves et al., 1983; Chesser, 1983; Smith et al., 1983). The geographic subdivision of a species can result in the genetic differentiation among its subpopulations. Stochastic events or differential selection pressures may be the causes of such heterogeneity (Smith et al., 1983; King et al., 1985; Brown, 1986). Currently there is a need to study the effect that geographic subdivision has on the genetic structure of populations. This type of information may provide useful insights into the speciation process and will have practical applications in conservation via the design of breeding programs and refuges (Chesser et al., 1980; Simberloff and Abele, 1982).

Notropis topeka has a disjunct distribution in six Central Plains states from southeastern South Dakota and southern Minnesota south to central Kansas and Missouri (Bailey and Allum, 1962; Cross, 1970; Gilbert, 1980; Phillips et al., 1982). Notropis topeka is confined to small intermittent headwater streams of the first and second order. This distribution has resulted in numerous

reproductively isolated populations within, as well as between, the Arkansas River and Kansas River drainage systems. Historically, N. topeka was found throughout Kansas in the Arkansas River and Kansas River drainage systems (Minckley and Cross, 1959). The extant populations in Kansas are restricted to the Flint Hills region in east central Kansas, and to one disjunct locality in extreme western Kansas (Cross, 1967; Platt et al., 1973; Schwilling, 1981). In recent years the preferred habitat of N. topeka has been subjected to increased levels of human alteration. Minckley and Cross (1959) postulated that the extirpation of central Kansas populations may have been due to groundwater losses caused by irrigation and increased siltation caused by the agricultural shift from grazing to intensive row crop farming. In 1978, N. topeka was listed as a threatened species by the Kansas Fish and Game Commission (Hlavachick, 1978). However, in 1987 its status was changed to "in need of conservation".

The elimination of good prairie headwater stream habitat has increased the isolation among the remaining populations of N. topeka, which may further reduce the amount of gene flow between populations. The disruption of gene flow may lead to increased amounts of inbreeding and decreased levels of heterozygosity within populations. The effects of heterozygosity at individual loci have

been documented for many species (Pierce and Mitton, 1982; Allendorf et al., 1983; Leary et al., 1983; Danzman et al., 1986). These studies indicated that genetic heterozygosity was correlated with an increased developmental rate that conferred higher reproductive fitness and survival to individuals heterozygous at specific loci. Therefore, the reproductive success of more genetically homogeneous populations may not equal their reproductive potential and threaten population survival. Population isolation may also lead to increased genetic differentiation among populations. The effects of this may not be completely disadvantageous. Although heterozygosity might be relatively low within a given population, the random fixation of alternate alleles in different populations can maintain the overall genetic variability of the species (Chesser et al., 1980).

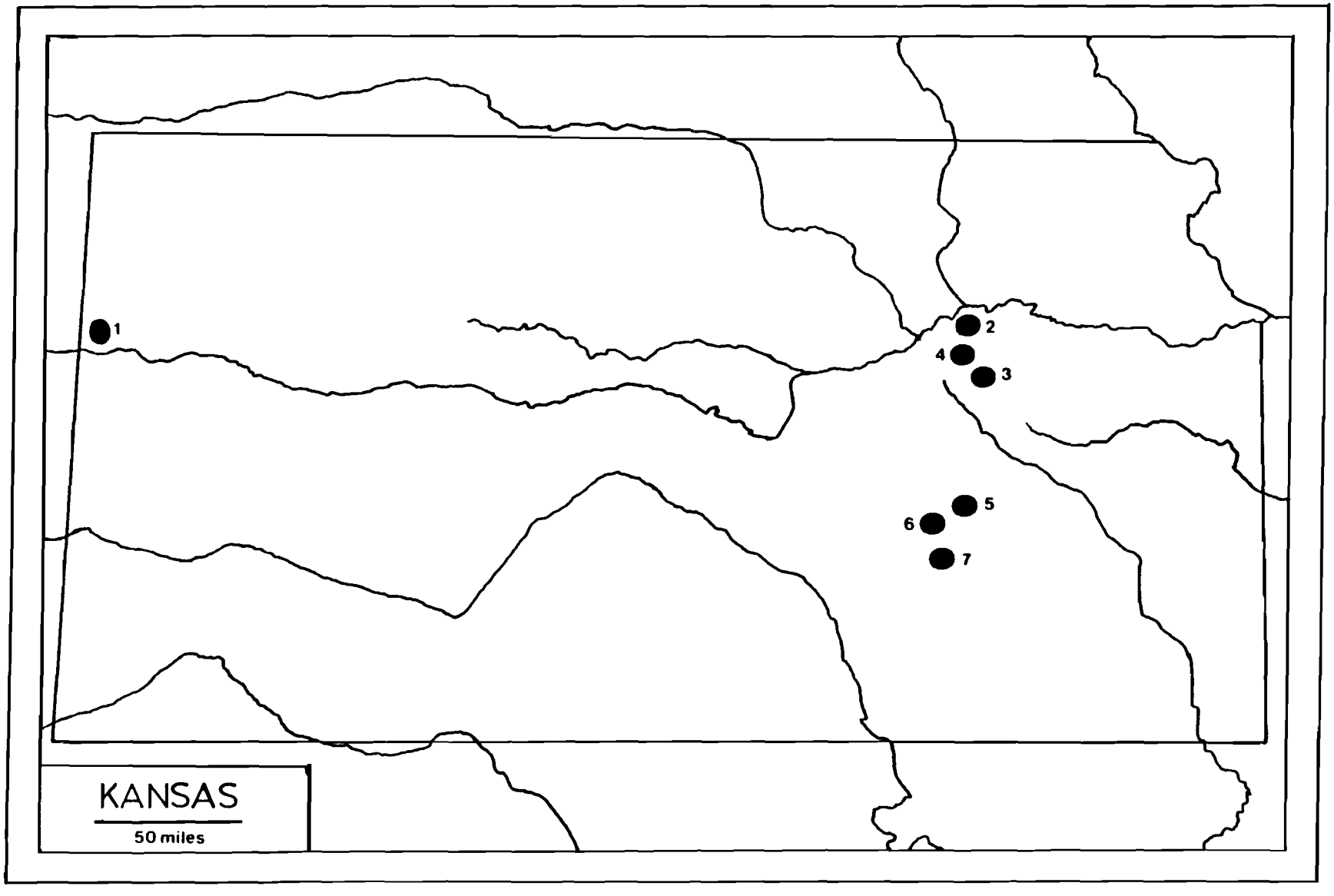
Information and publications on N. topeka consist almost exclusively of identification keys and lists of collection localities. The purpose of this study was to examine the level of genetic variation and determine the degree of genetic differentiation among populations of N. topeka in Kansas.

MATERIALS AND METHODS

Topeka shiners were seined from an extreme western Kansas locality (1) and from three sites each from the Kansas River drainage (2-4), and the Arkansas River drainage (5-7). Locality 1 was considered as a separate drainage because of the size and intermittency of the Smoky Hill River (Fig. 1). Identification numbers of the collection sites will be referred to throughout the remainder of the text. Locality number eight refers to a collection of N. lutrensis from the western Kansas locality that was used as an outgroup in the analyses. A total of 93 N. topeka were collected during June and July of 1986. Specimens were labeled according to location and frozen in liquid nitrogen. Upon return to the laboratory, whole fish were homogenized in a buffered saline solution and stored at -40 C until they were electrophoretically examined.

Genic variation in all specimens was examined by horizontal starch-gel electrophoresis at the following 21 loci. Malate dehydrogenase (MDH-1, MDH-2, MDH-3), malic enzyme (ME), lactate dehydrogenase (LDH-1, LDH-2), sorbitol dehydrogenase (SDH-1, SDH-2), and glucose-6-phosphate dehydrogenase (G-6-PDH) were determined on tris-citrate buffer of pH 8.0. Esterase (EST-1), glycerol-3-phosphate dehydrogenase (GPD-1, GPD-2), alcohol dehydrogenase (ADH-1, ADH-2), peptidase leucyl-glycyl-glycine (PEP-1), peptidase leucyl-glycine (PEP-2),

Fig. 1--Map of collection sites of *Notropis topeka* in Kansas. 1-Wallace Co., 2-Riley Co., 3 and 4-Wabaunsee Co., 5 and 6-Chase Co., 7-Butler Co.


1
2
4
3
5
6
7
KANSAS
50 miles

peptidase leucyl-leucyl-leucine (PEP-3, PEP-4), phosphoglucomutase (PGM-1), and glucose phosphate isomerase (GPI-1, GPI-2) were determined on lithium hydroxide buffer with gel pH 8.4 and electrode pH 8.1. The electrophoretic techniques, buffers and stains follow those of Selander et al., (1971).

Loci were scored by designating the most anodally migrating allele as "A". All other alleles at a locus were assigned alphabetic designations in order of decreasing anodal mobility. Loci were considered polymorphic if the frequency of the common allele in at least one population was less than 0.95. Heterozygosity (H) was determined from direct counts of heterozygous genotypes.

Chi-square goodness-of-fit tests were used to test for homogeneity of allele frequencies at the six most variable loci across populations and among drainages. Subchi-square values provided an index of genic differentiation attributable to within population and within drainage uniqueness, respectively. The simultaneous test procedure outlined by Sokal and Rohlf (1981) was used to identify homogeneous sets of populations from the total (seven) and homogeneous sets of drainages from the total (three) by chi-square analysis. Exact significance probabilities were calculated using a 2 x 2 contingency table to test whether each population was

in accord with Hardy-Weinberg equilibrium at all variable loci. Levene's (1949) correction for small sample sizes was used.

The degree of genetic differentiation among the seven populations of N. topeka was analyzed by F-statistics (Wright, 1965; Nei, 1977). Chi-square analysis was used to test for the significance of F_{ST} values for each locus following Workman and Niswander (1970), and for F_{IS} values following Nei (1977). All F-values were calculated using means and variances of allele frequencies weighted by sample sizes. F_{IS} and F_{IT} measure the degree of genetic differentiation of an individual from the expected Hardy-Weinberg proportions of its subpopulation and the total population, respectively. F_{ST} measures the degree of genetic differentiation among the subpopulations from the expected Hardy-Weinberg proportions of the total population. The F_{ST} for multiple alleles is equivalent to Nei's G_{ST} (Wright, 1978). A hierarchical analysis of population differentiation was performed that partitioned the heterogeneity into within locality, among locality, and among drainage components (Wright, 1978).

Rogers' (1972) genetic similarity and Nei's (1972) genetic distance were calculated for all pairwise comparisons of populations. A phenogram summarizing the genetic relationships among the populations was constructed from the genetic similarity matrix using the

UPGMA algorithm (Sneath and Sokal, 1973). The relationship between linear geographic distance and genetic distance was analyzed using the general regression approach described by Mantel (1967). Statistical analyses were performed using the computer programs of Pimentel and Smith (1985), Swofford and Selander (1981), and Ploskey (1985).

RESULTS

The allele frequencies for 10 polymorphic loci, and Hardy-Weinberg results for each population are presented in Table 1. Three loci (MAL-1, GPI-1, G-6-PDH) were polymorphic in all samples. Unique alleles for EST-1 and ADH-2 were found in populations 4 and 6, respectively. Twenty-one of 38 tests deviated significantly from Hardy-Weinberg equilibrium. Mean levels of heterozygosity ($\bar{H}$) ranged from 0.015 (site 1) to 0.065 (site 5). The mean level of H was 0.048 for populations in the Arkansas River drainage and 0.041 for Kansas River drainage populations, with a mean of 0.039 among all populations. The proportion of polymorphic loci varied from 0.143 (site 1) to 0.333 (sites 4, 5, 7), with a mean of 0.276 (sites 1-7).

Chi-square tests indicated that allele frequencies were not distributed homogeneously among sites or among drainages (Tables 2 and 3). Table 4 reports the results of the simultaneous test procedure (STP) among populations. Only GPI-1/D indicated that the significance of the heterogeneity of allele frequencies was due to a limited number of populations (1 and 3). The STP for results among river drainages ($P < 0.05$) indicated that the Arkansas River drainage was in the same homogeneous subset with the western Kansas drainage and the Kansas River drainage 47% and 15% of the time, respectively. The Kansas drainage was in the same subset with the western

TABLE 1--Allele frequencies of 10 variable loci for *Notropis topeka* collected in Kansas. Significant deviation from Hardy-Weinberg equilibrium is indicated by asterisks. Mean heterozygosity ($\bar{H}$) and percent polymorphic loci (P) are listed for each population. Refer to Fig. 1 for locality designations.

	locus			
Site	ME-1	G-6-PDH	EST-1	ADH-2
1		A/0.187**		
	B/0.219**	B/0.187		
	C/0.781	C/0.625	B	A
	N=16	N=16	N=16	N=16
2		A/0.143		
	B/0.429*	B/0.500		
	C/0.286	C/0.214		
	D/0.286	D/0.143	B	A
	N=7	N=7	N=7	N=7
3		A/0.375**		
	B/0.875	B/0.500		
	C/0.125	C/0.125	B	A
	N=8	N=8	N=8	N=8
4	A/0.187**	A/0.857**	A/0.062*	
	B/0.812	B/0.143	B/0.937	A
	N=16	N=14	N=16	N=13

*P < 0.05, **P < 0.01, ***P < 0.001

TABLE 1--Continued.

5		A/0.357**		
	A/0.036	B/0.036		
	B/0.429	C/0.536		
	C/0.536	D/0.071	B	A
	N=14	N=14	N=14	N=14
6		A/0.250***		
	B/0.312	B/0.250		A/0.937*
	C/0.687	C/0.500	B	B/0.062
	N=16	N=16	N=16	N=16
7		A/0.600***		
	B/0.733*	B/0.067		
	C/0.267	C/0.333	B	A
	N=15	N=15	N=16	N=16

*P < 0.05, **P < 0.01, ***P < 0.001

TABLE 1--Continued.

Site	locus			
	PEP-1	PEP-2	PEP-3	PEP-4
1				B/0.937
	B	B	B	C/0.062
	N=16	N=16	N=16	N=16
2	B	B	B	B
	N=7	N=7	N=7	N=7
3	A/0.250*			A/0.125
	B/0.750	B	B	B/0.875
	N=8	N=8	N=5	N=8
4				A/0.594***
	A/0.437***			B/0.312
	B/0.562	B	B	C/0.094
	N=16	N=14	N=7	N=16
5	A/0.077*		A/0.077*	
	B/0.923	B	B/0.923	B
	N=13	N=14	N=13	N=14

*P < 0.05, **P < 0.01, ***P < 0.001

TABLE 1--Continued.

6		A/0.062***		
		B/0.750		A/0.031
	B	C/0.187	B	B/0.969
	N=16	N=16	N=13	N=16
7	B/0.937*	A/0.125**	A/0.083	A/0.156
	C/0.062	B/0.875	B/0.917	B/0.844
	N=16	N=16	N=6	N=16

*P < 0.05, **P < 0.01, ***P < 0.001

TABLE 1--Continued.

Site	locus GPI-1	locus GPI-2	$\bar{H}$	P
1	B/0.250***		0.015	19.0
	C/0.625			
	D/0.125	B		
	N=16	N=16		
2	A/0.286		0.034	14.3
	B/0.214			
	D/0.500	B		
	N=7	N=7		
3	B/0.437		0.030	23.8
	D/0.562	B		
	N=8	N=8		
4	A/0.267	A/0.094	0.044	33.3
	B/0.300	B/0.875		
	D/0.433	F/0.031		
	N=15	N=16		
5	B/0.679	B/0.964	0.065	33.3
	D/0.321	G/0.036		
	N=14	N=14		

*P < 0.05, **P < 0.01, ***P < 0.001

TABLE 1--Continued.

6	A/0.062		0.036	28.6
	B/0.719			
	D/0.219	B		
	N=16	N=16		
7	A/0.031		0.044	33.3
	B/0.594			
	D/0.375	B		
	N=16	N=16		

*P < 0.05, **P < 0.01, ***P < 0.001

TABLE 2--Results of chi-square test for homogeneity of allele frequencies among all populations of *Notropis topeka* collected in Kansas. Refer to Fig. 1 for locality designations.

Locus/ allele	chi-square (d.f. = 6)	% of chi-square 1	2	3	4	5	6	7
ME-1/B	20.378**	28.3	1.3	18.0	24.2	2.5	13.7	11.9
ME-1/C	35.897***	29.3	1.5	9.0	36.8	2.8	16.3	4.3
PEP-1/B	5.422	9.6	4.2	5.7	67.8	1.0	9.6	2.2
PEP-2/B	1.892	8.2	3.6	4.0	7.1	7.1	63.5	6.5
PEP-4/B	13.053*	3.6	3.8	0.3	78.7	7.7	5.9	0.1
GPI-1/B	14.686*	23.7	13.9	0.4	13.6	16.0	26.4	6.1
GPI-1/D	10.247	40.2	11.7	25.1	9.2	0.1	12.0	1.8
G-6-PDH/A	24.765***	15.7	9.9	0.2	54.7	0.8	8.2	10.5
G-6-PDH/C	23.351***	24.9	3.8	10.9	44.0	9.3	6.6	0.4
Total	149.691***							

*P < 0.05, **P < 0.01, ***P < 0.001

TABLE 3--Results of chi-square test for homogeneity of pooled allele frequencies of Notropis topeka among river drainages in Kansas (site 1-Western Kansas drainage, sites 2, 3, and 4-Kansas River drainage, sites 5, 6, and 7-Arkansas River drainage). Refer to Fig. 1 for locality designations.

		% of chi-square		
Locus/ allele	chi-square (d.f. = 2)	Western Kansas drainage	Kansas drainage	Arkansas drainage
ME-1/B	11.449**	50.4	47.4	2.2
ME-1/C	27.166***	38.7	55.3	6.1
PEP-1/B	3.150	16.5	65.2	18.3
PEP-2/B	0.829	18.0	32.6	49.5
PEP-4/B	5.195	8.9	66.7	24.4
GPI-1/B	13.330**	26.2	24.6	49.3
GPI-1/D	8.493*	48.5	49.1	2.4
G-6-PDH/A	6.709*	58.0	41.6	0.4
G-6-PDH/C	20.206***	28.8	61.6	9.6
Total	103.995***			

*P < 0.05, **P < 0.01, ***P < 0.001

TABLE 4--Results of the simultaneous test procedure analysis for the six most variable loci for populations of Notropis topeka collected from Kansas. Significant heterogeneity was determined by chi-square contingency tests ($P < 0.05$). Refer to Fig. 1 for locality designations.

Locus/allele	Locality						
ME-1/B	3	4	7	2	5	6	1
ME-1/C	1	6	5	2	7	3	4
PEP-1/B	1	2	6	7	5	3	4
PEP-2/B	1	2	3	4	5	7	6
PEP-4/B	2	5	6	1	3	7	4
GPI-1/B	6	5	7	3	4	1	2
GPI-1/D	3	2	4	7	5	6	1
G-6-PDH/A	4	7	3	5	6	1	2
G-6-PDH/C	1	5	6	7	2	3	4

Kansas drainage 23% of the time. None of the allele frequencies were homogeneous across all drainages.

The genetic similarity values between pairs of populations are given in Table 5 and are summarized in a phenogram (Fig. 2). The phenogram indicated that populations do not cluster strictly by drainage and that the extreme western Kansas population is genetically more similar to the populations from the Arkansas River drainage.

The general regression approach described by Mantel (1967) indicated a significant linear correlation ($F = 4.67$, d.f. = 1, 40) between Nei's (1972) genetic distance and linear geographic distance between localities (Fig. 3). However, distance explained only 10% of the variation ($r^2 = 0.10$, $r = 0.32$). Genetic distance between pairs of populations is given in Table 5.

Results of the analysis of the standardized variance of allele frequencies indicated significant differentiation among all populations of N. topeka (Table 6). This indicates that there is significant genetic subdivision within this species. On average about 22% ($\overline{F_{ST}} = 0.219$) of the total variance of allele frequencies was due to differences among N. topeka populations. Thus, 78% of the total gene diversity was attributable to differences among individual fish within any given population ($1-\overline{F_{ST}}$). Significant heterogeneity was not

TABLE 5--Matrix of Nei's (1972) genetic distance (above diagonal) and Rogers' (1972) genetic similarity (below diagonal) based on 21 presumptive loci. Refer to Fig. 1 for locality designations. Locality 8 refers to *Notropis lutrensis*.

SITE	1	2	3	4	5	6	7	8
1	*****	0.029	0.049	0.095	0.018	0.017	0.035	0.565
2	0.932	*****	0.011	0.057	0.017	0.019	0.019	0.607
3	0.904	0.941	*****	0.026	0.021	0.030	0.009	0.638
4	0.852	0.888	0.918	*****	0.061	0.078	0.032	0.640
5	0.939	0.935	0.924	0.874	*****	0.003	0.006	0.555
6	0.948	0.933	0.912	0.855	0.953	*****	0.015	0.544
7	0.913	0.928	0.945	0.900	0.950	0.935	*****	0.572
8	0.558	0.538	0.518	0.518	0.558	0.567	0.549	*****

Fig. 2--Phenogram (UPGMA) based upon Rogers' (1972) genetic similarity values summarizing the genetic relationships among populations of Notropis topeka collected in Kansas. Refer to Fig. 1 for locality designations.

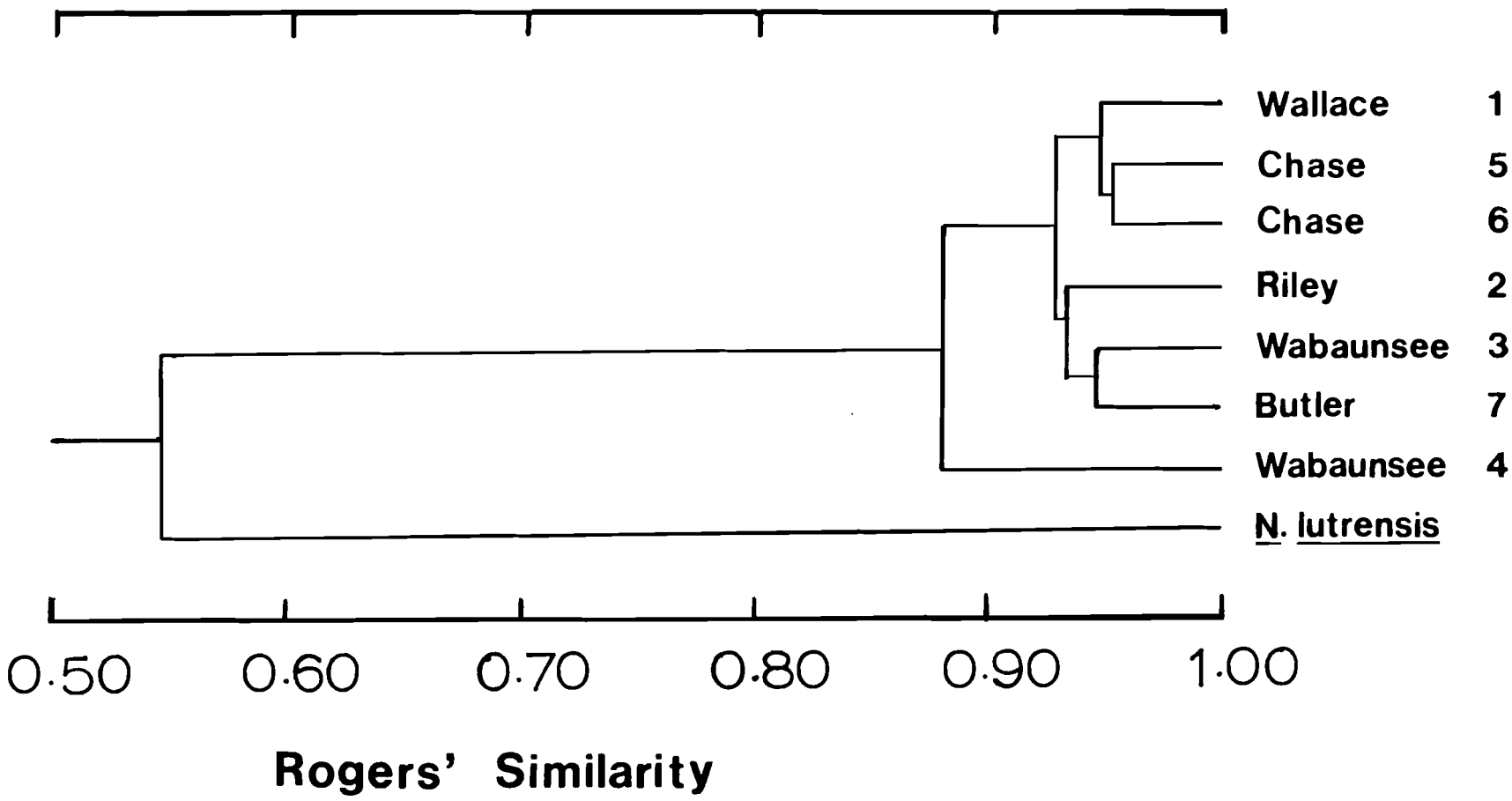

Wallace 1
Chase 5
Chase 6
Riley 2
Wabaunsee 3
Butler 7
Wabaunsee 4
N. lutrensis
0.50
0.60
0.70
0.80
0.90
1.00
Rogers' Similarity

Fig. 3--Plot of Nei's (1972) genetic distance versus linear geographic distance for 42 pairwise combinations of seven localities of Notropis topeka. Refer to Fig. 1 for locality designations.

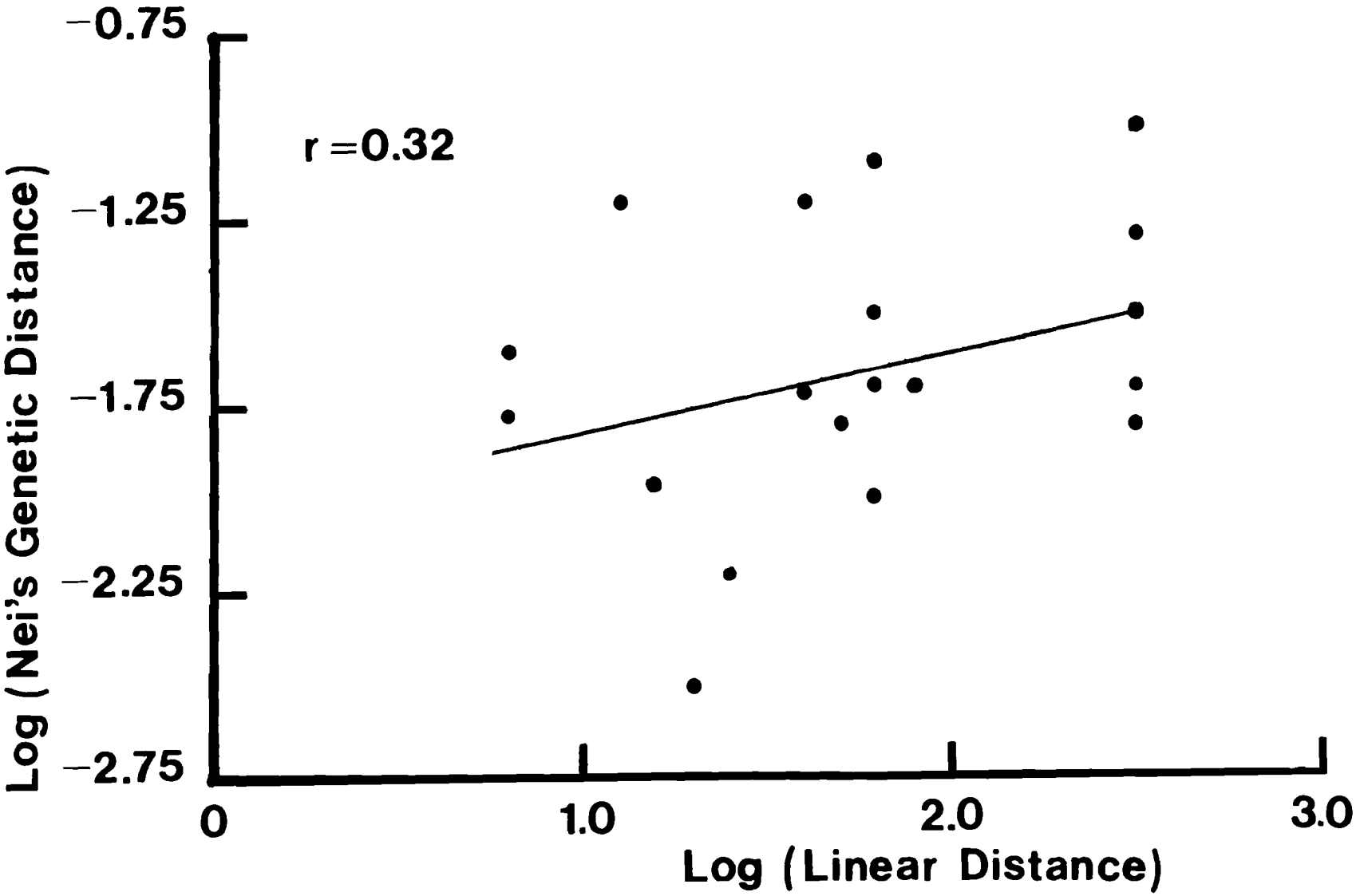

−0.75
−1.25
−1.75
−2.25
−2.75
r =0.32
Log (Nei's Genetic Distance)
0
1.0
2.0
3.0
Log (Linear Distance)

TABLE 6--Results of the F-statistics analysis for each variable locus for populations of Notropis topeka collected in Kansas. Significance of F_{IS} and F_{ST} values indicated by chi-square value.

Locus	F_{IT}	F_{IS}	chi-square	F_{ST}	chi-square	d.f.
ME-1	0.738	0.645	38.3**	0.261	141.3***	18
EST-1	1.000	1.000	93.0***	0.054	9.1	6
ADH-2	1.000	1.000	90.0***	0.054	8.9	6
PEP-1	1.000	1.000	92.0***	0.235	84.6***	12
PEP-2	1.000	1.000	91.0***	0.143	49.5***	12
PEP-3	0.468	0.435	12.7*	0.059	7.0	6
PEP-4	0.729	0.584	31.7**	0.348	127.6***	12
GPI-1	0.250	0.079	0.6	0.186	99.4***	18
GPI-2	0.379	0.331	10.2	0.072	37.4**	18
G-6-PDH	0.928	0.910	74.5***	0.201	105.3***	18
Mean	0.689	0.602	534.0***	0.219	670.1***	126

*P < 0.05, **P < 0.01, ***P < 0.001

found at three polymorphic loci. Two of those loci (EST-1, ADH-2) have unique alleles in different populations with the other populations fixed for the most common allele. The significantly high positive F_{IS} values for all polymorphic loci except GPI-1 and GPI-2 indicated that there was, on average, a deficiency of heterozygous individuals within each population. This indicates that potentially high levels of inbreeding are occurring within each population. The high positive F_{IT} values indicated that fewer heterozygous individuals than expected were found when all populations were pooled. A separate hierarchical analysis indicated the following partitioning of the total gene diversity; 81% within population diversity, 15% among population diversity, and 4% among drainage diversity. These data compare well with the above F-statistic results.

Results of the separate analyses of the standardized variance of allele frequencies for the Arkansas River and Kansas River drainage indicated significant genic differentiation among populations within the same drainage (Table 7). However, it seems that there is less differentiation among those populations inhabiting the Arkansas River drainage.

A summary of the F_{IS} values calculated for each population at all polymorphic is presented in Table 8. No locus had negative F_{IS} values in all populations, but

GPI-1 accounted for four the of nine negative values. Also, no negative F_{IS} values were significantly different from zero.

TABLE 7--Results of the F-statistics analysis for each variable locus for populations of Notropis topeka collected in the Kansas River and Arkansas River drainages in Kansas. Significance of F_{ST} indicated by chi-square value.

Drainage	locus	F_{ST}	chi-square	d.f.
Kansas	ME-1	0.167	28.1***	6
	EST-1	0.043	1.7	2
	PEP-1	0.182	10.3**	2
	PEP-4	0.382	45.4***	4
	GPI-1	0.046	3.5	4
	GPI-2	0.070	6.7	4
	G-6-PDH	0.205	32.7***	6
	Mean	0.178	128.3***	28
Arkansas	ME-1	0.121	19.8***	4
	ADH-2	0.043	2.9	2
	PEP-1	0.037	4.7	4
	PEP-2	0.092	14.9**	4
	PEP-3	0.028	0.8	2
	PEP-4	0.078	6.2	2
	GPI-1	0.016	0.9	4
	GPI-2	0.024	1.2	2
	G-6-PDH	0.064	14.3*	6
	Mean	0.067	65.7***	30

*P < 0.05, **P < 0.01, ***P < 0.001

TABLE 8--Compilation of F_{IS} values calculated for each population of Notropis topeka, for all polymorphic loci.

	Western Kansas drainage	Kansas River drainage	Arkansas River drainage	Total
# of chi-square analyses	4	15	19	38
# of negative F_{IS} values	1	2	6	9
# of F_{IS} values significantly different from zero *	3	11	10	24

*P < 0.05

DISCUSSION

Notropis topeka is restricted to patches of prairie headwater streams throughout its range. The results of this study indicate that a large degree of genetic differentiation has occurred among the Kansas populations. The amount of genetic differentiation reported here ($\overline{F_{ST}}$ = 0.219) is relatively high when compared to values reported for other vertebrate species (Nei, 1975 p.152; Zimmerman et al., 1980; Chesser, 1983; King et al., 1985). The high F_{ST} values along with the presence of unique alleles indicates genetic subdivision of the populations and substantial amounts of inbreeding. The evidence of inbreeding is not surprising considering the polygynous mating system of N. topeka (Pflieger, 1975). However, the reported mean values of heterozygosity and polymorphism are similar to those for other specialist species (Nevo, 1978). Also, it is interesting that even with substantial heterogeneity among populations only about 4% of this is due to differences among the drainages. Frye and Leonard (1952) reported that the last connection between the Kansas River and Arkansas River drainages occurred during the Illinoian between the ancestral Smoky Hill River and the Little Arkansas River. Several scenarios could be developed to explain the limited amount of genetic differentiation among the drainages. It may be that selection pressures among the present drainages are similar, or that N. topeka is a

narrowly adapted species. There may still be some stream capture of headwater streams near the divide of the drainages during periods of high water. Perhaps the small amount of genetic differentiation attributable to differences among drainages is due to the relatively short duration of time the drainages have been separated. The effects of chance alone may also explain the observed differences.

An isolation by geographic and ecological distance model of gene flow seems the best approximation for the distribution of N. topeka (Wright, 1943; Mayr, 1970). Since the early 1900's the extirpation of populations of N. topeka has occurred. As populations were extirpated the geographic and ecological distances among the existing populations increased. These events may have reduced or eliminated gene flow between and among the remaining populations, which is supported by the high F_{ST} (0.219). Thus, the weak but statistically significant linear correlation between Nei's (1972) genetic distance and linear distance (Fig. 3) may only be a remnant of a stronger correlation that existed before the reduction of N. topeka distribution in Kansas.

From the results of this study two important managerial aspects should be considered; 1) management practices might best be benefitted if those populations of N. topeka having the lowest levels of heterozygosity ($\bar{H}$)

are most aggressively protected, and populations with higher levels of $\bar{H}$ used as source populations for future restoration projects; 2) extreme care should be taken in any restocking efforts to avoid the admixture of genetically distinct populations that could inevitably cause the loss, to some degree, of the available genetic resource inherent to *N. topeka*.

SUMMARY

This study reports the first extensive genic analysis for *N. topeka*. Seven populations of *N. topeka* were sampled throughout their Kansas distribution. Horizontal starch-gel electrophoresis was used to examine genic variation at 21 loci. Mean heterozygosity was greatest in the Arkansas River drainage, followed by the Kansas River drainage, and lowest in the disjunct population. Chi-square analysis and F-statistics indicated significant differences among populations in allele frequencies for the six most variable loci. In addition, averages of Rogers' genetic similarity values for the populations in the Arkansas River drainage were 0.946 and 0.916 for populations in the Kansas River drainage. There was also a weak, but statistically significant, correlation between linear distance and Nei's genetic distance. Suggestions for managerial practices are given.

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