THE GENETIC STRUCTURE OF OKLAHOMA POPULATIONS OF THE COLLARED LIZARD, CROTAPHYTUS COLLARIS

By

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INTRODUCTION

The purpose of this study was to use horizontal starch-gel electrophoresis to examine inter- and intrapopulation genetic variation within collared lizards (Crotaphytus collaris) in Oklahoma. Although limited genetic study has been conducted on this species at the extreme periphery of its range in Missouri (Templeton, 1986; Templeton et al., 1990), no study has examined the genetic structure of the species in the central part of its range, which includes Oklahoma.

Because recent studies have uncovered a mosaic of sexual dimorphism (McCoy et al., 1994; Baird, et al., In press; McCoy et al., In press) and consequently suggested a parallel mosaic of sexual selection among three populations of collared lizards in Oklahoma (McCoy, 1995), this study also examined two of the three previously studied localities and a new locality to see if genetic structuring of populations may help to explain the complex pattern of sexual selection that has been suggested.

Differences in sexual dimorphism among three populations of collared lizards in Oklahoma have been examined previously (McCoy et al., 1994; McCoy et al., In press). In each population, females and males differ in both body size and coloration; in general, males are larger and more brightly colored. There are marked differences, however, in the degree and pattern of dimorphism among populations. Certain traits are more dimorphic in some populations and other traits are more so in other populations. The distinctly different patterns of morphology, coloration, and degree of dimorphism among the three populations suggest the action of differential selection, most likely differential

sexual selection. Variation in ecological conditions can influence the degree and type of sexual selection (Slatkin, 1984), which in turn can influence sexual dimorphism. Indeed, there are strong ecological differences among the three sites. These differences may lead to variation in predation and social organization, aspects that ultimately could lead to the evolution of the varied pattern of sexual dimorphism observed at present. In support of this hypothesis, prior field and laboratory work on these three populations show that social organization, predation, and degree and type of sexual selection vary among them (Baird et al., In press).

At the phenotypic level, sexual dimorphism within and among the three populations is obvious and the pattern is complex. But what does this imply about the genetic aspects of these populations? Is there similarly complex variation at the genetic level? Are the populations genetically differentiated? If so, the genetically distinct populations may be the root source of the observed patterns of phenotypic sexual dimorphism. Answers to these questions would allow a better understanding of the observed mosaic pattern of sexual dimorphism in this species.

At the extreme eastern periphery of its range in Missouri, populations of collared lizards in the Ozarks have been isolated for approximately 4000 years. The various populations are small (50 individuals or less) and genetic drift over the 4000 years has resulted in fixed differences among populations and lack of genetic variation within them (Templeton, 1986; Templeton et al., 1990). Do populations of collared lizards in Oklahoma also exhibit a lack of genetic variation? Genetic variability is necessary for adaptation and long-term survival of a species; it allows utilization of habitats that are

diverse temporally and spatially. Populations lacking sufficient genetic variation may become extinct if environments change too drastically. Examination of the genetic structure of collared lizards in the central part of their distribution can determine levels of genetic variation and also reveal information about the amount of genetic exchange among populations, and past changes (primarily reductions) in population sizes.

The goals of this study were to: 1) describe patterns of geographic variation in allelic and phenotypic frequencies; 2) estimate the degree of genetic distance among geographically separated populations in Oklahoma; 3) estimate the relative importance of random drift and gene flow in these populations; and 4) because recent studies have uncovered a mosaic of sexual dimorphism and consequently suggested a parallel mosaic of sexual selection among three populations in Oklahoma (McCoy et al., 1994), examine two of the three localities (plus a new one) to seek genetic differences among the populations (i.e., a genetic basis for the complex pattern of sexual selection that has been suggested).

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LITERATURE REVIEW

Study Animal

The Eastern collared lizard Crotaphytus collaris collaris (Family Crotaphytidae), also known as the mountain boomer, is a diurnal, territorial lizard with two black collar markings on its neck (Seivert and Seivert, 1993). Eastern collared lizards extend from east and south central Missouri into northern Arkansas; south into central Texas; and north into eastern New Mexico and southeastern Colorado (Conant and Collins, 1991). Collared lizards are found throughout Oklahoma (Seivert and Seivert, 1993), which lies within the central core of the species' distribution.

Differences in morphology and coloration between the sexes contribute to the sexual dimorphism of collared lizards. Collared lizards are relatively large lizards with a total length of 203-356 mm and snout-vent length of up to 115 mm (Conant and Collins, 1991). Males are generally larger than females in body mass (Yedlin and Ferguson, 1973; Rostker, 1983; Sexton et al., 1992; McCoy et al., 1994;), have greater snout-vent length (Rostker, 1983; McCoy et al., 1994), larger head width, wider tail base, and longer tail length (Bontrager, 1980; Rostker, 1983).

Coloration and pattern of the collared lizard varies throughout the distribution of the species. Males may have colors of yellow, green, brown, and blue on the body with light spots on the dorsum, and yellow to yellow-orange coloration on the throat. Females and subadult males are similar in coloration but are much less brilliant than adult males. Their scales are generally of dull colors: browns, grays, and yellows (Woodbury, 1952),

and young males commonly have a series of dark crossbands on their dorsum (Conant and Collins, 1991). In Oklahoma, males typically are blue-green to olive green and have a golden throat coloration. Females are typically tan with a white throat. Both sexes have the speckled pattern of light spots on their dorsal side. Juveniles generally are brown to yellow with dark bars on their body (Seivert and Seivert, 1993).

Collared lizards inhabit many diverse habitats in arid and semi-arid regions and generally are associated with rocky, open habitats. Limestone ledges, rock piles (Conant and Collins, 1991), rocky outcrops on impoundment dams (Seivert and Seivert, 1993), and any other type of topographic projections are used for basking, as lookout posts (Bontrager, 1980; Conant and Collins, 1991), and for other activities such as courtship and copulation (Yedlin and Ferguson, 1973). These rocky habitats also provide crevices for escape and for use during inactivity (Bontrager, 1980; Conant and Collins, 1991). Barriers such as valleys between mountains (Smith and Tanner, 1974) or habitat fragmentation via the encroachment of forest habitats, such as in the Ozarks (Missouri), can isolate populations from one another (Templeton et al., 1990).

Genetic Differentiation of Local Populations

Differences in morphological characteristics (Patton and Smith, 1989; Baker et al., 1990; Baughman et al., 1990; Pigliucci et al., 1990; Hillis et al., 1991; McCoy et al., 1994), coloration (Luyton and Liley, 1991; McCoy et al., 1994) and behavior (Luyton and Liley, 1991) among geographically adjacent populations of various species have been documented. Not all species showing phenotypic differences among geographically

separated populations, however, will show congruent patterns of genetic differences (Baughman et al., 1990; Hillis et al., 1991). The pattern of genetic diversity in a species primarily is determined by three evolutionary forces: gene flow, natural selection, and genetic drift (Slatkin, 1981; Allendorf, 1983). These forces also can interact with historical factors, such as climate and geology (Baughman et al., 1990). Any one force or combination of forces may play a greater role or have a greater effect at different times and locations, influencing the distribution of genetic variation within and among populations.

Gene flow, which is the movement of alleles among and between populations, can increase variation within a population by bringing in novel alleles. Gene pools of populations that have continuous gene flow between them become similar and the likelihood of differentiation of allele frequencies among populations is reduced (Baker et al., 1990). Barriers to gene flow on a microgeographic scale, such as restricted genetic exchange between local groups because of social structure, such as in house mice (Mus musculus; Selander, 1970) or because of differences in breeding habitat, such as in host-specific insects (Nuculapsis californica; Edmunds and Alstad, 1978), can result in genetic differentiation of populations. On a larger scale, geographic barriers such as mountains and rivers can limit gene flow, which in turn can separate and isolate populations from one another (Pounds and Jackson, 1981). When genetic exchange becomes limited over large geographic distances, selection and random drift primarily are responsible for changes that occur within the populations (Liu and Godt, 1983). Both forces can reduce the overall genetic diversity of populations, particularly small, isolated ones (Bonnell and

Selander, 1974).

Genetic differentiation of local populations can occur also through differential selection pressures, even though it may appear that there is no barrier to gene flow. Selection, however, must be strong enough to counteract the effect of genetic exchange (Liu and Godt, 1983). There can be different selective regimes in different habitats because environmental conditions are infinitely variable. Natural selection promotes adaptation to local conditions, and thus, when selective regimes differ among geographically separated populations, genetic differentiation among populations can occur (Liu and Godt, 1983; Smith et al., 1983).

Selection also may play a role in creating genetic differentiation among populations that have experienced a reduction in size. It is possible for the gene pools of these populations to be different. A difference in the gene pools means that natural selection will have different raw materials upon which to work. These populations, therefore, have different capabilities for change and are likely to experience genetic (and phenotypic) differentiation, depending on the overall as well as the interacting effects of selection, gene flow, and genetic drift (Emlen, 1973).

Genetic drift (or random drift) can cause genetic differentiation among populations by creating differences in allelic frequencies among the populations (Hartl, 1994). Genetic drift is a change in the allele frequency of a gene pool due to chance events (Hartl, 1981). It results from random sampling among gametes from one generation to the next (Ayala and Kiger, 1984; Hartl, 1994). The occurrence of differential genetic drift among geographically isolated populations can result in

differences in genetic composition and, therefore, also differences in phenotypes among populations (Emlen, 1973). Small populations are more likely to suffer sampling error due to the greater chance that rare genotypes might not be passed on to the next generation (Ayala and Kiger, 1984). Thus, small populations are more susceptible to the loss of genetic variability and are likely to diverge more rapidly than populations of large size (McClenaghan and Beauchamp, 1986; Hartl, 1994). Populations that have experienced bottleneck and founder events are both likely to be affected by random drift.

Bottleneck and founder events are periods when a population is reduced to only a few individuals and genetic drift has a potent effect on gene pool frequencies. Both result in a reduction in population size and both events accelerate the process of drift, often to the loss or fixation of alleles (i.e., a reduction of heterozygotes). Genetic bottlenecks can happen following unfavorable climatic or other environmental conditions or following natural disasters (such as fire) and can reduce the proportion of polymorphic loci through the loss of rare alleles (Nei et al., 1975; Allendorf, 1986). Such populations are subjected to near extinction and if the population size does recover later, it may be that the allelic frequencies were altered considerably during the bottleneck. Founder effect also results in only a few types of genotypes contributing to the next generation and chance alone is responsible for which alleles are carried by the founders. The gene pool of the population, because of its reduction in the number of individuals, is also much smaller. If drift occurs among several small, isolated populations simultaneously, it then becomes possible for the gene pools to diverge (Ayala and Kiger, 1984).

Additionally, inbreeding commonly occurs in populations that have undergone a

severe reduction in size. Inbreeding, which results from mating between relatives, reduces genetic variability by decreasing the frequency of heterozygotes. Thus, the effect of inbreeding is similar to that of random drift; both result in the loss of one or the alternative allele. South African cheetahs (O'Brien et al., 1983; O'Brien et al., 1985), northern elephant seals (Bonnell and Selander, 1974), snub-nosed monkeys (Su and Shi, 1995), and collared lizards (Templeton, 1986; Templeton et al., 1990) are examples of species that have suffered a reduction in genetic variation due to drift and inbreeding following bottleneck and/or founder events.

In general, the effect of random drift on populations that have undergone bottlenecks and/or founder events and subsequent inbreeding is that these populations tend to lose genetic variability (Bonnell and Selander, 1974; O'Brien et al., 1983; O'Brien et al., 1985; Templeton, 1986; Templeton et al., 1990). A reduction in genetic variability is accomplished by decreasing the frequency of heterozygotes and/or the proportion of polymorphic loci (Nei et al., 1975; Allendorf, 1986). Thus, heterozygosity (H), which is the average frequency of heterozygous individuals at a locus, and polymorphism (P) are both measures that are used to quantify genetic variation (Ayala and Kiger, 1984). Findings of significant heterozygote deficiencies and/or reductions in the number of alleles per locus may suggest the occurrence of bottlenecks and/or founder events (Nei et al., 1975; O'Brien, et al., 1983, 1985).

Sexual Selection

Secondary sexual characters can occur in morphology, coloration, and behavior of

organisms and may be due to one or more of the following: differences between the sexes in the use of ecological niches (Slatkin, 1984; Hedrick and Temeles, 1989), differences between the sexes in their reproductive roles, and/or sexual selection (Vitt and Cooper, 1985; Hedrick and Temeles, 1989; Vial and Stewart, 1989; Luyton and Liley, 1991).

Sexual selection, which generally results in some form of sexual dimorphism, is the selection for traits involved only with increasing mating success (Darwin 1871; O'Donald, 1980; Krebs and Davies, 1993). Darwin (1871) formulated the theory of sexual selection to explain how sexually dimorphic traits may evolve and how they influence the chances of mating. Darwin's theory explains the origin and maintenance of secondary sex characters, particularly in males, that may even be detrimental to survival.

Sexual selection can be separated into two components: intrasexual selection, which is competition between members of one sex (usually males) for access to (i.e., fertilization of) the other sex (Darwin, 1871; Krebs and Davies, 1993); and intersexual selection (epigamic selection), which operates by mating preferences (Darwin, 1871; Krebs and Davies, 1993). Males develop characters that are attractive to females and females choose males with those characters. The two components of sexual selection often operate at the same time. (Krebs and Davies, 1993).

Although Darwin provided evidence for the existence of female mating preference, he did not explain how such a character evolved (Kirkpatrick, 1982; Andersson, 1986). There are several theories that attempt to explain exaggerated secondary sexual characters, primarily in males, and the evolution of female preference (Hedrick and Temeles, 1989). The evolution of preference could be based entirely on

viability differences (Andersson, 1986); selective factors, such as direct selection on male traits by predators (Houde and Endler, 1990); because females are able to choose a mate that is of high genetic quality, and thereby produce offspring that are healthier and have a better chance of survival (Emlen, 1973; Ghiselin, 1974; Zahavi, 1975; Hamilton and Zuk, 1982); or because of a mating advantage (Fisher, 1958). Fisher (1958), using population genetic terminology, was able to explain how elaborate traits came about by outlining a mechanism of the evolution of female preference and of sexual dimorphism (Krebs and Davies, 1993). His model, also called the "runaway" process of sexual selection, was an elaboration of Darwin's concept of sexual selection. The Darwin-Fisher theory of sexual selection was further developed and expressed mathematically (O'Donald, 1962, 1967) and in terms of quantitative genetics (Lande, 1981; Kirkpatrick, 1982). The models of quantitative genetics, in particular, have been used to explain differences in secondary sexual traits in males of related species (Lande, 1981), and also may explain variation in sexual dimorphism among geographically separated populations.

According to Fisher, the evolution of male secondary sexual traits is directly affected by female mating preferences. Female preference can evolve if there is a slight initial survival advantage of the male trait which happens to be preferred by females (O'Donald, 1962, 1967, 1980; Andersson, 1986). Females receive a selective advantage by mating with the fittest males. Females must, therefore, be able to discriminate among males. Those females that are able to discriminate and mate with fitter males will gain a selective advantage over females that do not discriminate (O'Donald, 1980).

Genetic covariance between the male trait and female preference for the male trait

is an important component in Fisher's runaway process (Lande, 1981). An association (covariance) between the expressed character and preference for it would arise because females will mate nonrandomly based on their preference for certain traits (Lande, 1981; Kirkpatrick, 1982). Although all offspring from this cross possess both the trait and preference genes, the trait is expressed only in males and the preference (for the trait) in females (Krebs and Davies, 1993). Thus, both genes (trait and preference genes) are passed down and increase in the population due to the enhanced survival of sons that have the trait. Males that possess the trait will also gain a mating advantage as the preference for the trait spreads. The males' trait may evolve an evermore exaggerated condition that may subsequently carry even a survival disadvantage. The two traits will continue to evolve until a balance between a reduction in male survival and mating advantage has been reached (Andersson, 1986) or the frequency of the allele for the male trait can continue to increase (O'Donald, 1962, 1967) and may even become fixed in the population (Kirkpatrick, 1982) regardless of the consequent reduction in survivorship. The initial gene frequencies, which ultimately determine the level of covariance, as well as the genetics of the trait, both determine the rate at which female preference is selected (O'Donald, 1967, 1980).

Theoretical studies of quantitative population genetics have further shown that epigamic traits do not necessarily need to be initally adaptive and that weaker forces, such as pleiotropy and genetic drift, may also give rise to female preference (Lande, 1981; Kirkpatrick, 1982). Female preference for a certain trait may be due initially to pleiotropic effects; the genes were selected for some other purpose (Emlen, 1973). Other

chance events that occur at the start of the coevolution of the two traits (the male trait and the female preference for the trait) also can result with the traits evolving in a runaway fashion (Emlen, 1973; Lande, 1981). Male traits may come to be genetically preferred by females and chance alone may increase the frequency of this female preference to the point where epigamic sexual selection rapidly effects the coevolution of male traits and female preference for them (Lande, 1981; Kirkpatrick, 1982). Such a scenario would be favored by conditions that promote stochastic genetic change, i.e., founder effect and genetic drift.

The ecology of Oklahoma collared lizards suggests that such stochastic effects may well be at work. Colonies of these lizards are patchily distributed only on rocky outcrops, separated by expanses of unsuitable habitat. Some colonies are small and occasionally undergo severe changes in density (Fox, in litt.). Thus, both founder effect and genetic drift may be important in molding the genetics of these colonies. Because each colony may be differentially affected, epigamic sexual selection could "run away" with a different assemblage of traits for each population, and the resultant populations would show a mosaic of sexual dimorphism -- a condition described in Oklahoma populations of collared lizards (McCoy et al., 1994; McCoy et al., In press).

METHODS

Collection of Animals

I collected collared lizards during May - June, 1993, and May - July, 1994, from various sites within three localitites: Wichita Mountains National Wildlife Refuge (Comanche County; n = 126) located in southwestern Oklahoma; Glass Mountains (Major County; n = 86) located in northwestern Oklahoma; and Sooner Lake (Noble County; n = 37) in northcentral Oklahoma. Six populations were sampled from the Wichita Mountains (WMAA - WMFF), five from the Glass Mountains (GMA, GMB, GMCE, GMD, and GMF), and two from Sooner Lake (SSDAM and SSOON). I also made a small collection from Ten Acre Rock (TAR; Johnston County; n = 5) in southcentral Oklahoma. I collected a total of 254 individuals from 14 populations. Lizards were captured live by noose and tail biopsies were taken by dissecting approximately 1.5 cm off the tip of the tail. Tissues were frozen at -70° C for up to several months prior to use. I released animals unharmed at point of capture.

Description of Study Sites

Collared lizards in the Glass Mountains were found on gypsum outcrops ringing the tops of steep buttes. Wheat fields and prairies surround these buttes, fragmenting the suitable habitat. Lizards in the Wichita Mountains were found on large, pervasive granite outcrops. These outcrops are extensive and interconnected, which permits movement of lizards over large distances. Thus, unlike the Glass Mountains, there is

much more suitable habitat available at the Wichita Mountains. Lizards from the Sooner Dam population (SDAM) were found on boulders imported to construct the dam; lizards from the Sooner population (SSOON) were found on an isolated sandstone outcrop. The two Sooner Lake populations were separated by mostly unsuitable prairie habitat and by Sooner Lake itself. Ten Acre Rock is a pre-Cambrian granite boulder surrounded by oak-hickory forests. Collared lizards in this locality are restricted to the boulder or to smaller granite outcrops that extend into the forest. The distance between localities averaged 197.1 km (140.1 - 268.9 km) (Figure I). The distance between populations at Sooner Lake was 4.0 km. The distances between populations at the Glass Mountains and Wichita Mountains localities ranged from 0.7 - 12.0 km and 1.1 - 16.5 km, respectively.

Electrophoresis

I used conventional methods of horizontal starch gel electrophoresis to resolve and expose allozymic variation within and among collared lizard populations for 16 enzyme systems and general protein loci (Table I). Prior to electrophoresis, all tissue samples were diluted 1:1 with distilled water, homogenized, and centrifuged for 15 seconds. I used five buffer systems: Tris-citrate, pH 6.7; Tris-citrate, pH 7.5; Tris-citrate-EDTA, pH 7.0; Tris-borate-EDTA, pH 8.6; and Lithium hydroxide, pH 8.3 (Selander et al., 1971; Hillis and Moritz, 1990). All gels had a starch concentration of 11.5%; a current of 45-55 mA was used to facilitate the separation of proteins. Run time for gels ranged from 9 - 16 hours.

I examined 21 individuals per gel. Twenty-five individuals, however, were

placed on each gel. The four additional positions, which were used to help maintain consistency in scoring enzyme phenotypes, were occupied by one randomly selected individual. The same individual was used for all runs and was positioned at slots 1, 9, 17, and 25 on each gel. I included several individuals from different sites on the same gel to eliminate any bias associated with locality. The recipes for the protein stains are described by Selander et al. (1971) and Hillis and Moritz (1990). Gels were fixed in a 5:5:1 ethanol-water-acetic acid solution following the staining procedure.

I designated the most common allele at each locus as M. Alleles faster than M were designated as F. Alleles slower than M were designated as S. Alleles that migrated differently from these three main alleles were designated by letters preceding or following the letters F, M, or S with the convention that A was the very fastest and Z was the very slowest. For example, there may have been an allele that was defined as a "fast" allele but it may not have migrated as far as the F allele. This allele I designated as G. Alleles that were slower than G, I designated as H, and so forth. If there was a "fast" allele that migrated farther (i.e., faster) than the F allele, it was designated as E. Alleles that migrated farther than E were designated as D, and so on.

Population Genetics

I used a direct count of phenotypes on the gel to obtain genotypic frequencies. I then used BIOSYS-1 (Swofford and Selander, 1981) to determine allele frequencies and levels of heterozygosity and polymorphism, test for conformance to Hardy-Weinberg expectations, and calculate F-statistics and distance coefficients. Genetic variability for

each population was examined by estimating mean number of alleles per locus, mean heterozygosity, and the mean percentage of polymorphic loci. A locus was considered polymorphic if the frequency of the most common allele was less than or equivalent to 0.95 (i.e., polymorphism was defined based on a 95% criterion). Significant differences in mean heterozygosity and polymorphism among localities were determined using Kruskal-Wallis Chi-square tests (Sokal and Rohlf, 1981).

I used Wright's F-statistics (Wright, 1969, 1978) to examine hierarchical structure and levels of genetic differentiation among populations of collared lizards by analyzing standardized genetic variance across all polymorphic loci. A heterogeneity chi-square analysis (Workman and Niswander, 1970) was used in conjunction with the F-statistics to examine heterogeneity in allele frequencies among populations. I also used Chi-square analyses (Li and Horvitz, 1953; Workman and Niswander, 1970) to test null hypotheses $F_{is} = 0$ and $F_{st} = 0$. Values that differed significantly from zero indicated deviation of heterozygote proportions from Hardy-Weinberg expectations.

Rogers' genetic distance (Rogers, 1972) was used to examine genetic relationships among populations. The matrix produced by Rogers' distance measure was used for cluster analysis. I used unweighted pair group method with arithmetic averaging (UPGMA) to derive a phenogram that described the relationship among populations of collared lizards. I employed Mantel's test (1967) to test for a significant correlation between the matrix of genetic distance and geographic distance among all pairs of populations.

I used two methods to estimate gene flow among collared lizard populations. The

first method was Wright's (1931) island model, which used F_{st} values to estimate Nm (the number of migrants exchanged per generation). The equation for this model is: Nm = $[(1/\bar{F}_{st} - 1]/4$. By using F_{st} values, I estimated gene flow at different hierarchical levels. The second method I used employed private allele frequencies (Slatkin, 1985). The equation for this model is: $Nm^* = e^{(-[(\ln \bar{p}(1)] + 2.44)]/0.505}/\bar{N}/25$, where $\bar{p}(1)$ represents the average frequency of all private alleles (i.e., alleles found in only one population), and $\bar{N}$ represents the average number of individuals sampled per population.

Recent studies on collared lizards have revealed differences in sexual dimorphism and morphological characters (McCoy et al., 1994; McCoy, 1995; Baird, et al., In press; McCoy et al., In press)) among two localities in Oklahoma (Glass Mountains and Wichita Mountains). I expected collared lizards from these localities to show congruent genetic differences. Because of the ecology of collared lizards, bottleneck and founder events (and therefore, genetic drift) ought to be common and to have an effect on the genetic diversity of these populations, bringing about significant differentiation among populations. I also expected a significant association between geographic and genetic distance. Populations within a locality, however, should not be similarly differentiated because of common, similar habitat (and therefore similar selection pressures) and because higher levels of gene flow should occur between populations within localities than among localities.

The null hypotheses tested were: 1) genetic variability (heterozygosity and proportion of polymorphic loci) among populations is the same; 2) populations are not genetically differentiated from other populations within the same locality; 3) populations

within a locality are not genetically differentiated from populations from another locality; 4) genetic distance is unrelated to geographic distance; 5) gene flow estimates among populations within a locality are the same, and 6) gene flow estimates among localities are the same.

RESULTS

Within-Population Genetic Variability

For all 21 loci surveyed, the allele most common overall was found in every population either at the highest, or second highest, frequency. Of these 21 loci, 12 were monomorphic and nine were polymorphic. All populations were monomorphic for the same 12 loci (AK, CK, GOT-2, GP-1, GP-2, GPD, IDH-2, LDH-1, MDH-1, MDH-2, PEP-D, and PGM) and were fixed for the same allele. Allele frequencies for the nine loci found to be polymorphic (GOT-1, GPI, IDH-1, LDH-2, MDHP, PEP-B, PEP-Z, PGDH, and PK) are given in Table II. I detected two alleles at GOT-1, IDH-1, and LDH-2; three alleles at GPI, MDHP, PEP-B, PEP-Z, and PK; and four alleles at PGDH. Although GPI, MDHP, and PEP-Z were polymorphic for most samples, they were fixed in some populations. Apparently, the GPI locus is fixed in two populations (SSOON and TAR), the MDHP locus is fixed in the Ten Acre Rock sample, and PEP-Z is fixed in three Glass Mountains populations (GMB, GMD, and GMF).

The number of alleles per locus varied little among populations (Table III), ranging from 1.1 to 1.4 alleles. The mean number of alleles per locus was 1.3. I detected at least one "private" allele in six of the 14 sites sampled (Table II). I found three private alleles in the Glass Mountains (MDHP F-allele, PEP-B F-allele, and PEP-Z S-allele), and three in the Wichita Mountains (GPI T-allele, IDH-1 F-allele, and PK F-allele). I also observed two alleles at two loci that were found in more than one population but were unique to a locality: the F-alleles at the GOT-1 and LDH-2 loci were found in several

populations only in the Glass Mountains.

The loci showing most variability were GPI, MDHP, PEP-B, PEP-Z, and PGDH (Table II). Some variability was seen at the GOT-1 and LDH-2 loci. The frequency of the most common allele ranged from 0.868 to 0.925 for GOT-1 and 0.750 to 0.897 for LDH-2. Rare variability was seen in IDH-1 and PK, with the frequency of the most common allele as 0.947 for IDH-1 and a range of 0.950 to 0.981 for PK (Table II).

To detect deviations from Hardy-Weinberg equilibrium, I employed a Chi-square test to compare observed and expected genotypic frequencies for all polymorphic loci. Levene's (1949) correction for small sample size was used to calculate expected values. Four of the 73 independent chi-square tests performed showed significant deviations (alpha = 0.05) from Hardy-Weinberg expectations: PGDH from site SSDAM ($p < 0.001$), PGDH from site GMA ($p = 0.014$), MDHP from site GMB ($p = 0.001$), and GPI from site GMD ($p = 0.004$). Thus, 5.5% (4/73 = 0.055) of the tests performed indicated nonconformance to Hardy-Weinberg expectations. All significant deviations from Hardy-Weinberg equilibrium were heterozygote deficiencies. The proportion of deviations is marginally significant but does approximate what would be expected at the 5% significance level if sampling error alone was responsible for the deviations.

The percentage of polymorphic loci ranged from 14.3 in the Ten Acre Rock sample to 28.6 in four samples (GMB, GMD, WMBB and WMFF) (Table III). The overall proportion of polymorphic loci across populations was 23.8. Heterozygosity ranged from 0.049 at Ten Acre Rock to 0.119 at GMB (Table III). The overall mean heterozygosity was 0.096.

Among the four localities I sampled, genetic variability was low in the Ten Acre Rock sample (H = 0.049; P = 14.3) compared to the other three localities: Sooner populations ($\bar{H}$ = 0.086-0.106, $\bar{X}$ = 0.096; P = 19.0-23.8, $\bar{X}$ = 21.4), Wichita Mountains ($\bar{H}$ = 0.094-0.110, $\bar{X}$ = 0.101; P = 19.0-28.6, $\bar{X}$ = 24.6), and Glass Mountains ($\bar{H}$ = 0.079-0.119, $\bar{X}$ = 0.100; P = 23.8-28.6, $\bar{X}$ = 25.7) (Table 3). The mean estimates for heterozygosity and polymorphism for Sooner Lake, Glass Mountains, and Wichita Mountains localities were not significantly different ($X^2_{2, 0.05}$ = 0.28, p = 0.87 and $X^2_{2, 0.05}$ = 2.29, p = 0.32, respectively).

Among-Population Genetic Variability

I quantified genetic differentiation among populations using Wright's F-statistics (Wright 1969, 1978), Chi-square contingency analyses, and Rogers' genetic distance (Rogers, 1972). Considering Wright's F-statistics, F_{it}, the overall inbreeding coefficient, measures departures of genotypic frequencies from Hardy-Weinberg expectations by combining all individuals from all samples. It quantifies the reduction in heterozygosity, which reflects the amount of inbreeding due to the combined effects of nonrandom mating within populations (F_{is}) and to genetic drift among populations (F_{st}). Mean F_{it} was 0.17, with values ranging from -0.03-0.31 (Table IV).

F_{is}, the inbreeding coefficient, measures reduction in heterozygosity within a population due to nonrandom mating. F_{is} values range from -1 to 1. Zero indicates that genotypic frequencies do not deviate from Hardy-Weinberg expectations. F_{is} values for all samples across all polymorphic loci ranged from -0.26-0.12. Mean F_{is} was 0.03,

which was not significantly different from Hardy-Weinberg expectations ($X^2_{1, 0.05}$ = 0.069, $0.90 < p < 0.95$) (Table IV). A test for heterogeneity among F_{is} values across all polymorphic loci for all populations was significant ($X^2_{8, 0.05} = 26.41$, $p < 0.005$). The only locus that showed significant deviations from Hardy-Weinberg expectations in heterozygote frequencies was LDH-2 ($X^2_{1, 0.05} = 17.30$, $p < 0.005$). LDH-2 had more heterozygotes than expected. When this LDH-2 locus was removed from the set, no significant heterogeneity in F_{is} was found among the remaining polymorphic loci across all populations.

To test for significant differences in tendencies of deficient or excess levels of heterozygotes, a Sign test was used to compare counts of positive and negative F_{is} values among populations for each of five polymorphic loci (GPI, MDHP, PEP-B, PEP-Z, and PGDH). PEP-Z, which had an excess of heterozygotes, was the only locus that showed significant nonrandom departures ($X^2_{1, 0.05} = 4.45$, $0.025 < p < 0.050$). Tests for the GOT-1, IDH-1, LDH-2, and PK loci could not be conducted due to small sample sizes.

F_{st}, a measure of genetic differentiation among populations, was used to estimate the amount of divergence of allelic frequencies among populations. F_{st} can be interpreted in terms of random genetic drift in an ideal population that has no mutation, selection, or migration. Hartl (1981) gives a qualitative interpretation of F_{st} values: 0.00-0.05 indicates little genetic differentiation; 0.05-0.15 indicates moderate differentiation; 0.15-0.25 indicates great differentiation; and > 0.25 indicates very great differentiation.

F_{st} across all 14 populations ranged from 0.03 (PK) to 0.21 (MDHP and PEP-Z) (Table IV). All polymorphic loci, except for PK, showed significant population

differentiation; F_{st} values were significantly different from zero. The results of Chi-square contingency analysis for allele heterogeneity for each locus across all 14 populations were congruent with F_{st} measures (Table IV). Thus, all loci except PK showed significant departures from Hardy-Weinberg expectations among populations. A test for heterogeneity among F_{st} values across all nine polymorphic loci was not significant ($X^2_{8, 0.05} = 10.42$, $0.10 < p < 0.25$). Mean F_{st} across all polymorphic loci for all 14 populations was 0.14, i.e., 14% of the genetic variance was due to differentiation among the 14 populations, while 86% of the genetic variance occurred within the populations. Based on Hartl's interpretation, genetic heterogeneity over all 14 samples indicated moderate, bordering on great, population differentiation.

Chi-square contingency analyses revealed significant differentiation among populations within localities for several polymorphic loci. There was an overall significant differentiation across all loci among populations in the Glass Mountains ($X^2_{44, 0.05} = 88.76$; $p < 0.001$). By locus, there was significant differentiation among populations there for LDH-2 ($X^2_{4, 0.05} = 17.72$; $p = 0.001$) and PEP-Z ($X^2_{8, 0.05} = 23.03$; $p = 0.003$). The F-allele at the LDH-2 locus is unique to the Glass Mountains locality and is present in two of the five samples. The PEP-Z locus is fixed for the M-allele in three of the five populations in the Glass Mountains, but in none of the populations at the other localities. Although the GOT-1 locus showed significant differentiation among all populations ($X^2_{8, 0.05} = 40.83$, $p < 0.001$; Table IV), mainly due to the presence of the A-allele that is unique to the Glass Mountains locality, no significant differences were found among the populations at just this locality at this locus. The Sooner Lake locality showed an overall

significant heterogeneity among populations ($X^2_{7, 0.05} = 19.90$; $p = 0.006$). Both GPI ($X^2_{1, 0.05} = 4.09$; $p = 0.04$) and PEP-B ($X^2_{1, 0.05} = 4.82$; $p = 0.03$) loci had significant heterogeneity among populations there. There was no significant differentiation among populations across all loci for the Wichita Mountains locality ($X^2_{55, 0.05} = 59.26$; $p = 0.32$). However, significant heterogeneity among populations was found there at the IDH-1 locus ($X^2_{5, 0.05} = 11.35$; $p = 0.05$).

I also examined F_{st} values for each locality to determine how differentiated the populations were within localities. The F_{st} values for the Sooner Lake, Glass Mountains, and Wichita Mountains localities were: 0.048, 0.056, and 0.017, respectively. This implies that little deviation from Hardy-Weinberg equilibrium was due to differentiation among populations at a locality (4.8%, 5.6%, and 1.7%, respectively), while most of the variance occurred within populations (95.2%, 94.4%, and 98.3%, respectively). A test for among-locality heterogeneity comparing F_{st} values shows no significant differentiation ($X^2_{2, 0.05} = 0.08$; $0.975 < p < 0.950$), indicating that similar levels of differentiation have taken place at all localities.

Population Structure

Hierarchical analysis (Wright, 1969, 1978) of population structure of C. collaris indicated that most (88.6%) of the total genetic diversity ($H_t = 0.108$) was due to within-population diversity, 9.6% was due to differences of allele frequency among localities, and 1.8% was due to differences among populations within localities.

Genetic Distance

I used Rogers' (1972) estimate of genetic distance (D) for pairwise comparisons of the 14 populations (Table V). Three major clusters were revealed in the phenogram (Figure 2): the five populations from the Glass Mountains are clustered together (D = 0.027-0.042), the six populations from the Wichita Mountains are clustered together (D = 0.01-0.025), and the two Sooner Lake populations are grouped together (D = 0.045) with the Ten Acre Rock sample (D = 0.065). The Glass Mountains and Wichita Mountains clusters/groups are separated by a distance of D = 0.058, and the Sooner/Ten Acre Rock cluster is separated from the Glass Mountains and Wichita Mountains cluster by a distance of D = 0.068. The overall levels of genetic distance among populations were low; genetic distances were all less than 0.068. The clusters, however, do reflect a distinct geographical pattern.

I used the Mantel (1967) test to determine if there was a significant correlation between the matrices of genetic distances and geographic distances between populations. This test revealed a significant association between genetic and geographic distances among all pairs of populations ($t_{\infty, 0.05} = 6.62$, $p < 0.001$), which suggests that stochastic factors, such as genetic drift and isolation-by-distance, have played an important role in the phenotypic and genotypic differentiation among populations of collared lizards.

Gene Flow

I used Wright's (1931) island model and Slatkin's (1985) "private allele" method to estimate gene flow among populations. The gene flow estimate, Nm, is the number of

migrants exchanged among populations per generation. N represents the effective population size and m represents the migration rate. Wright's method uses F_{st} values to derive estimates of gene flow, and Slatkin's method uses alleles that are "private" to only one population. The two methods do not always produce congruent results (Larson et al., 1984; Waples, 1987).

Using Wright's method, gene flow estimates for the Sooner Lake, Glass Mountains, and Wichita Mountains localities were 4.96, 4.21, and 14.46, respectively. The gene flow estimates using Slatkin's "private allele" method were 1.75, 3.15, and 7.25, respectively. Both methods reveal higher gene flow among populations in the Wichita Mountains. The gene flow estimate using the mean F_{st} (across all polymorphic loci for all populations sampled) of 0.14, was 1.54 individuals per population per generation, overall. Slatkin's estimate of overall gene flow for the total set of populations was 8.01 individuals per population per generation. Slatkin's method may have produced a higher mean estimate because of the high gene flow estimate from the Wichita Mountains locality.

Wright's method also was used to estimate gene flow among localities. Estimates of gene flow ranged from 1.27 (Sooner-Ten Acre Rock localities) to 3.27 (Ten Acre Rock-Wichita Mountains localities). These estimates are lower than the within-locality estimates; gene flow appears to be higher within localities than among localities.

DISCUSSION

Populations of collared lizards in Missouri, the eastern edge of the species' distribution, are small and have become isolated due to habitat fragmentation and forest encroachment. There is a lack of genetic variability within these Ozark populations (Templeton, 1986; Templeton et al., 1990). I expected populations of collared lizards in Oklahoma to be less isolated and have higher levels of genetic variability. I also expected genetic variability among these populations to be the same. Mean heterozygosity and polymorphism estimates were 9.6% and 23.8%, respectively. These estimates are within the range expected for an outcrossing population (Hartl, 1981). Variability estimates among Sooner Lake, Glass Mountains, and Wichita Mountains localities were not significantly different. Heterozygosity and polymorphism at Ten Acre Rock were considerably lower than the other three localities. This may be an artifact of small sample size. If considerable genetic drift, together with bottleneck or founder events had previously occurred within these populations of collared lizards, there would have been a significant reduction in mean heterozygosity or number of alleles (Allendorf, 1986). Reduced levels of heterozygosity and/or polymorphism, however, in general were not observed.

Genetic variability estimates from this study were slightly higher than several other species of lizards. Mean heterozygosity estimates for Lacerta sicula (mainland populations), Sceloporus undulatus hyacinthinus, and Uta stansburiana were 9.1% (Gorman and Nevo, 1975), 5.6% (Spohn and Guttman, 1976), and 5.0% (McKinney and

Turner, 1971), respectively. Heterozygosity estimates for Gambelia wislizeni, which is in the same family as Crotaphytus, were fairly low, ranging from 1.7 - 6.2% (Montanucci et al., 1975). Mean polymorphism for G. wislizeni, Podacris sicula (mainland populations), and S. u. hyacinthinus ranged from 7.4 - 25.9 (Montanucci et al., 1975), 14.3 - 23.8 (Capula, 1994), and 15.4 - 38.5 (Spohn and Guttman, 1976), respectively.

I used F-statistics to examine the genetic structure of populations and the amount of differentiation among populations. F_{is} values were used to examine the structure of populations by revealing levels of inbreeding, i.e., nonrandom mating within populations. The small proportion of deviations of heterozygote frequencies from Hardy-Weinberg expectations and low values of F_{is} indicated that populations were not inbred. A test for heterogeneity among F_{is} values for all populations across all polymorphic loci was significant. When LDH-2 was excluded, however, heterogeneity among F_{is} values disappeared. LDH-2 was the only locus with a significant deviation of heterozygote frequencies from Hardy-Weinberg expectations. There was an excess of heterozygotes at this locus, which could be explained on the basis of selection for heterozygotes, but not on the basis of inbreeding.

F_{st} values were used to describe genetic differentiation among populations. Because recent studies showed differences in sexual dimorphism of several morphological characters among populations of collared lizards in Oklahoma, I expected to find significant genetic differentiation among localities. I also expected little differentiation among populations within localities due to similar selection pressures and higher levels of gene flow. Populations of collared lizards in Oklahoma appear to be

influenced primarily by genetic drift and gene flow. The interaction of these two factors has resulted in moderate, bordering on great, genetic differentiation among populations. The average differentiation among populations was 14.0%. This percentage is much smaller compared to the very small and isolated Missouri populations, where the average differentiation among populations was 47.0% (Templeton et al., 1990), but still appreciable. Significant differentiation was found across all populations for all polymorphic loci except PK. On the other hand, Rogers' coefficient showed populations were overall genetically rather similar. Based on the hierarchical analysis, populations within a locality, as expected, were more similar than populations from among localities. Rogers' genetic distance revealed a geographic trend among populations, and Mantel's test also reflected a significant relationship between genetic and geographic distance. Populations that were geographically adjacent generally had higher levels of gene flow than populations more geographically distant. Even within a locality, Glass Mountains and Sooner Lake localities had significant differentiation across populations at two loci each (LDH-2 and PEP-Z; and GPI and PEP-B, respectively). Populations at the Wichita Mountains locality, however, did not have any significantly differentiated loci. This indicated that gene flow at the Wichita Mountains was much higher compared to the other two localities. The cluster analysis also did not group the populations for the Glass Mountains and Sooner Lake localities as tightly as the Wichita Mountains locality. This is congruent with the hypothesis that barriers to gene flow are weaker at these localities compared to those of the Wichita Mountains because suitable habitat was much more extensive and homogeneous in the Wichita Mountains than in the other two localities.

The hierarchical analysis revealed that while most of the variance was found within populations (88.6 %), there was appreciable variance among (9.6%) and within localities (1.8%). This differentiation within and among localities indicates that gene flow does not serve as a cohesive force. The amount of gene flow among populations (both within and among localities), however, apparently has been sufficient to prevent further genetic differentiation due to drift. The overall estimate for gene flow using Wright's method was 1.54. This means that in order to maintain a divergence level of $\bar{F}_{st}$ = 0.14 or higher, no more than 1.54 individuals per generation on average can be exchanged among populations. According to Wright (1931), one individual per population per generation is sufficient to balance the effect of random drift. Populations are not expected to diverge significantly solely via genetic drift if Nm is greater than one (Allendorf, 1983; Slatkin, 1985). However, natural selection can further differentiate populations with this rather low gene flow, especially among localities where selection pressures may be different.

Based on models of sexual selection, the evolution of secondary sex traits depends on the starting conditions in a population. These starting conditions refer to specific traits of males and the preference for those traits by females (Andersson,1994). In order for a male trait to spread throughout the population, preference for that trait must first increase in the population. Factors such as genetic drift, founder effects, pleiotropy, and differential natural selection all affect the starting conditions of populations. If drift, or any of the above factors or combinations thereof, occurred among several populations simultaneously, those populations could become genetically differentiated and could

have different starting traits and preferences (Kirkpatrick, 1982; Lande, 1981). Runaway selection could then follow different evolutionary trajectories in each population and result in populations differing substantially in secondary sex traits and preferences for them (Andersson, 1994).

Differences in patterns of sexual dimorphism in coloration and morphology among populations of collared lizards in Oklahoma have been observed (McCoy et al., 1994; Baird, et al., In press; McCoy et al., In press). Populations of collared lizards in this study were genetically differentiated. Although gene flow appears to occur among these populations, sufficient genetic drift has had the effect of creating moderate differentiation among populations. Presumably, this level of differentiation of putatively neutral allozymes indexes the similar differentiation of secondary sex traits. This moderate differentiation of these secondary sex traits, because it may have led to different starting conditions for sexual selection, could have resulted in the differential evolution of female preferences and preferred male traits among populations via differential runaway selection and may be responsible for the mosaic of sexual dimorphism observed presently among populations.

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APPENDICES

APPENDIX A

TABLES

Table I. Abbreviations of enzyme names (capital letters), protein names, enzyme commission (EC) numbers, and buffer systems used in electrophoretic analysis of collared lizard muscle tissue.

Protein Abbreviation	Protein Name	Commission Number	Buffer System
AK	Adenylate Kinase	2.7.4.3	Tris-citrate, pH 7.5
CK	Creatine Kinase	2.7.3.2	Tris-citrate-EDTA, pH 7.0
GP	General protein		Tris-citrate EDTA, pH 7.0
GPI	Glucose-6-phosphate Isomerase	5.3.1.9	Tris-citrate I, pH 6.7
GPD	Glycerol-3-phosphate Dehydrogenase	1.1.1.8	Lithium-borate/Tris-citrate, pH 8.3
GOT	Glutamate-oxaloacetate transaminase	2.6.1.1	Tris-borate-EDTA I
IDH	Isocitrate Dehydrogenase	1.1.1.42	Tris-citrate I, pH 6.7
LDH	Lactate Dehydrogenase	1.1.1.27	Tris-citrate-EDTA, pH 7.0
MDH	Malate Dehydrogenase	1.1.1.37	Tris-citrate I, pH 6.7
MDHP	Malate Dehydrogenase (NADP+)	1.1.1.40	Tris-citrate I, pH 6.7
PEP-B	Peptidase w/ leucyl-glycyl-glycine	3.4.-.-	Tris-borate-EDTA I
PEP-D	Peptidase w/ phenyl-alanyl-proline	3.4.-.-	Lithium-borate/Tris-citrate, pH 8.3
PEP-Z	Peptidase w/ leucyl-alanine	3.4.-.-	Tris-citrate I, pH 6.7
PGM	Phosphoglucomutase	5.4.2.2	Tris-citrate-EDTA, pH 7.0
PGDH	Phosphogluconate Dehydrogenase	1.1.1.44	Tris-citrate-EDTA, pH 7.0
PK	Pyruvate Kinase	2.7.1.40	Tris-citrate, pH 7.5

Table II. Allele frequencies of polymorphic loci for each population (sample size in parentheses).

		Sooner Lake			Wichita Mountains						Glass Mountains				
Locus	Allele	SSDAM (21)	SSOON (16)	TAR (5)	AA (19)	BB (19)	CC (27)	DD (22)	EE (19)	FF (20)	A (20)	B (34)	CE (8)	D (12)	F (12)
GOT-1	F										0.075	0.132		0.083	0.083
	M	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.925	0.868	1.000	0.917	0.917
GPI	M	0.881	1.000	1.000	0.605	0.658	0.648	0.568	0.658	0.700	0.700	0.574	0.750	0.792	0.750
	S	0.119			0.368	0.342	0.352	0.432	0.342	0.300	0.300	0.426	0.250	0.208	0.250
	T				0.026[+]										
IDH-1	F					0.053[+]									
	M	1.000	1.000	1.000	1.000	0.947	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
LDH-2	F											0.103		0.250	
	M	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.897	1.000	0.750	1.000
MDHP	F													0.042[+]	
	M	0.452	0.313	1.000	0.658	0.789	0.796	0.795	0.789	0.775	0.425	0.368	0.250	0.333	0.625
	S	0.548	0.688		0.342	0.211	0.204	0.205	0.211	0.225	0.575	0.632	0.750	0.625	0.375
PEP-B	F											0.044[+]			
	M	0.571	0.813	0.800	0.526	0.526	0.444	0.455	0.474	0.275	0.900	0.691	0.938	0.792	0.792
	S	0.429	0.188	0.200	0.474	0.474	0.556	0.545	0.526	0.725	0.100	0.265	0.063	0.208	0.208
PEP-Z	F										0.025[+]				
	M	0.643	0.469	0.900	0.895	0.947	0.963	0.818	0.895	0.950	0.975	1.000	0.875	1.000	1.000
	S	0.357	0.531	0.100	0.105	0.053	0.037	0.182	0.105	0.050			0.125		
PGDH	F	0.595	0.313	0.700	0.237	0.263	0.315	0.227	0.211	0.175	0.150	0.250	0.250	0.292	0.500
	M	0.357	0.625	0.300	0.526	0.632	0.574	0.591	0.579	0.550	0.625	0.471	0.688	0.458	0.333
	R	0.024		0.026											
	S	0.024	0.063		0.211	0.105	0.111	0.182	0.211	0.275	0.225	0.279	0.063	0.250	0.167
PK	F									0.025[+]					
	M	1.000	1.000	1.000	1.000	1.000	0.981	1.000	1.000	0.950	1.000	1.000	1.000	1.000	1.000
	S						0.019			0.025					

[+]alleles that are unique to only one sample

Table III. Genetic variability at 21 loci among all collared lizards sampled in 14 populations.

Population[a]	n[b]	Mean number of alleles per locus	Percentage of loci polymorphic	Mean heterozygosity[c]
SSDAM	21	1.3	23.8	0.106
SSOON	16	1.2	19.0	0.086
TAR	5	1.1	14.3	0.049
WMAA	19	1.4	23.8	0.110
WMBB	19	1.3	28.6	0.098
WMCC	27	1.3	19.0	0.094
WMDD	22	1.3	23.8	0.106
WMEE	19	1.3	23.8	0.100
WMFF	20	1.4	28.6	0.095
GMA	20	1.3	23.8	0.089
GMB	34	1.4	28.6	0.119
GMCE	8	1.3	23.8	0.079
GMD	12	1.4	28.6	0.116
GMF	12	1.3	23.8	0.096
Mean	18.1	1.3	23.8	0.096

[a] population designations are mentioned in the text
[b] sample size
[c] unbiased estimate of mean heterozygosity based on conditional expectations (Levene, 1949; Nei, 1978)

Table IV. Summary of F-statistics and contingency Chi-square analyses at all polymorphic loci.

Locus	F_{it}	F_{is}	F_{st}	X^2	p
GOT-1	-0.03	-0.11	0.07	40.83	0.0001
GPI	0.12	0.03	0.09	49.80	0.0033
IDH-1	-0.00	-0.06	0.05	24.84	0.0242
LDH-2	-0.03	-0.26	0.19	75.71	0.0000
MDHP	0.31	0.12	0.21	108.69	0.0000
PEP-B	0.16	-0.00	0.16	93.22	0.0000
PEP-Z	0.12	-0.10	0.21	121.11	0.0000
PGDH	0.14	0.07	0.08	71.45	0.0011
PK	-0.00	-0.03	0.03	20.86	0.7494
Mean	0.17	0.03	0.14	606.50	0.0000

Table V. Matrix of Rogers (1972) genetic distance coefficients among all pairs of populations.

Population[a]	SDAM	SOON	TAR	WMAA	WMBB	WMCC	WMDD	WMEE	WMFF	GMA	GMB	GMCE	GMD	GMF
SSDAM	-----	0.045	0.059	0.051	0.061	0.062	0.061	0.060	0.073	0.064	0.069	0.061	0.066	0.052
SSOON		-----	0.071	0.075	0.080	0.084	0.082	0.082	0.096	0.060	0.074	0.043	0.063	0.069
TAR			-----	0.067	0.063	0.064	0.070	0.062	0.076	0.077	0.090	0.075	0.079	0.048
WMAA				-----	0.019	0.021	0.019	0.013	0.030	0.046	0.045	0.054	0.060	0.041
WMBB					-----	0.011	0.020	0.012	0.026	0.051	0.057	0.058	0.068	0.047
WMCC						-----	0.016	0.011	0.021	0.055	0.058	0.064	0.069	0.047
WMDD							-----	0.010	0.028	0.060	0.058	0.066	0.078	0.058
WMEE								-----	0.020	0.050	0.056	0.059	0.068	0.049
WMFF									-----	0.057	0.066	0.073	0.074	0.056
GMA										-----	0.033	0.028	0.034	0.034
GMB											-----	0.052	0.027	0.042
GMCE												-----	0.046	0.050
GMD													-----	0.036
GMF														-----

[a] Population designations are given in the text.

APPENDIX B

FIGURES

Figure 1. Map of Oklahoma showing the locations sampled for Crotaphytus collaris. GM = Glass Mountains; SL = Sooner Lake; TAR = Ten Acre Rock; and WM = Wichita Mountains.

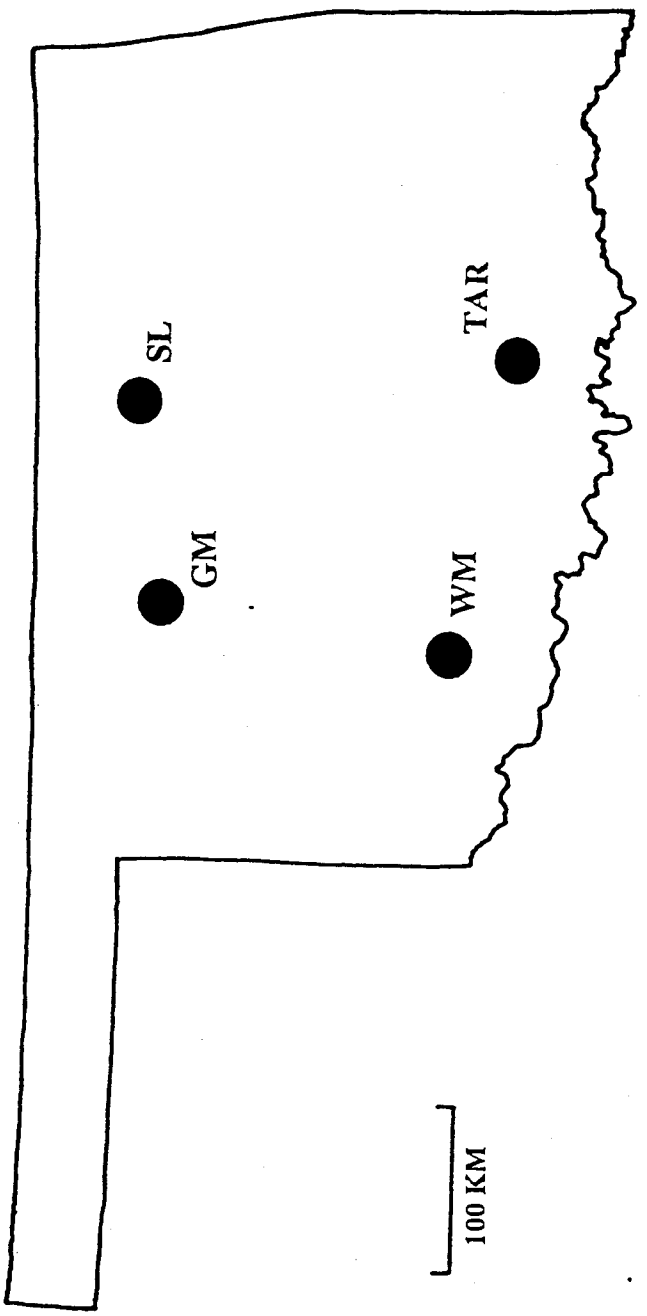
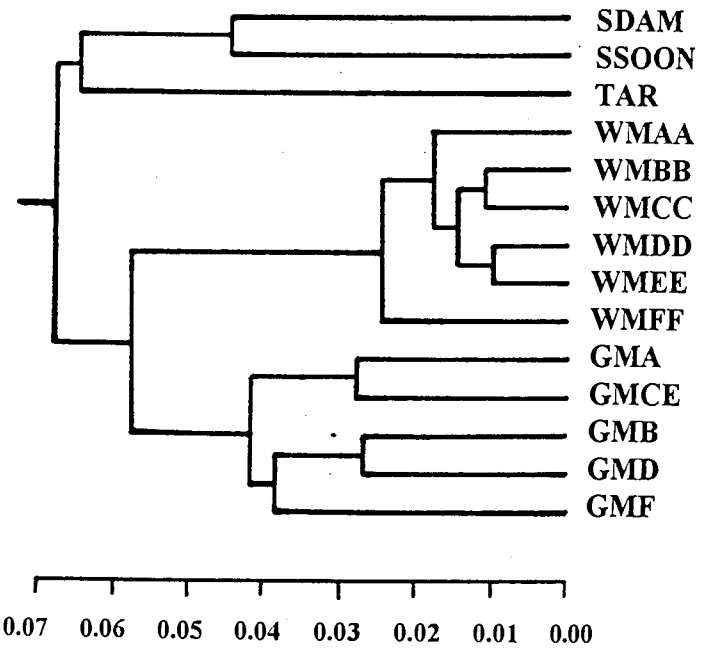

SL
TAR
GM
WM
100 KM

Figure 2. Dendrogram (UPGMA) of Crotaphytus collaris populations using Rogers' (1972) genetic distances. Population designations are given in the text.


SDAM
SSOON
TAR
WMAA
WMBB
WMCC
WMDD
WMEE
WMFF
GMA
GMCE
GMB
GMD
GMF
0.07
0.06
0.05
0.04
0.03
0.02
0.01
0.00

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