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**EXAMINING POPULATION STRUCTURE OF CISMONTANE AND
DESERT POPULATIONS OF ZEBRA-TAILED LIZARDS
(CALLISAURUS DRACONOIDES) USING MITOCHONDRIAL AND
NUCLEAR INTRON DNA.**

Lauren Nicole Morrison

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EXAMINING POPULATION STRUCTURE OF CISMONTANE AND DESERT
POPULATIONS OF ZEBRA-TAILED LIZARDS (*CALLISAURUS*
DRACONOIDES) USING MITOCHONDRIAL AND NUCLEAR INTRON DNA.

A Thesis
Presented to the
Faculty of
California State University,
San Bernardino

In Partial Fulfillment
of the Requirements for the Degree
Master of Science
in
Biology

by
Lauren Nicole Morrison

May 2024

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ABSTRACT

Callisaurus draconoides, also known as the Zebra-Tailed lizard, belongs to the family *Phrynosomatidae* family (Pianka, et al. 1972). *C. draconoides* is a widespread desert lizard found western North America. In California, this species can be found in the Mojave and Colorado Deserts. There are currently several populations that reside in the San Bernardino basin on the cismontane side of the Transverse and Peninsular ranges. These mountain ranges have the potential to have isolated the cismontane populations from their typical desert ranges. In addition, geological passes have the potential to serve as migration corridor between the Deserts and cismontane regions. The purpose of this research is to (1) determine if there are lineage breaks that are consistent with the geographic regions and (2) determine if the Cajon and Banning pass serve as migration corridors to the cismontane locations. Two mitochondrial and one nuclear molecular marker were utilized to elucidate the phylogenetic and population genetic structure as well as to examine the rarity of the cismontane populations. The significant phylogenetic and population genetic structure for the cismontane Zebra-tailed lizard populations demonstrated significance in the mitochondrial marker; however, not in the nuclear marker. These findings supported that isolation of the cismontane Zebra-tailed lizards was caused by a recent tectonic plate geological event (<750,000) (Matti & Morton, 1993). Therefore, it is argued that San Bernardino basin population constitutes a management unit of significance.

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DEDICATION

I dedicate this project to my father, Jay Morrison, who has served as a constant source of positivity and belief that I could anything I set my mind too. For helping me financially when I needed to work less and focus more time on my project. For going without so that I could have a chance at having something more. I would also like to dedicate this project to my mother, Kimberly Foglietta. My mom had the same belief as my father that I could do anything I set my mind and always encouraged me to reach for the stars. Her love was always a source of comfort, and I knew I could always count on her if I needed anything during this time. None of this would have been possible without the love and sacrifice both of my parents made for me to have more than they had. They both are my inspiration every day to be the best version of myself.

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CHAPTER ONE

INTRODUCTION

Overview

Understanding the entangled bank of biodiversity that Charles Darwin described in *The Origins of Species*, has challenged scientists for the past 150 years. In natural populations, numerous intertwined direct and indirect relationships contribute to the survivorship or organization of a population (Darwin, 1859). Another phenomenon that captivated Darwin was the diversity he observed in geographically structured populations. This phenomenon would continue to captivate biologists' interest in molecular phylogenetics and evolution today. The main forces that have been described to contribute to geographically structured populations are natural selection, mutation, migration (gene flow), and genetic drift. Phenotype alone is usually an inadequate explanation of geographic population structure. To investigate if distance was the sole contributor the population structure discussed, the use of neutral genetic markers allowed biologist to examine evolutionary relationships of such populations (Benson, 2006). Neutral genetic markers were utilize as a tool in molecular phylogeny studies because it allows for unbiased estimates of genetic diversity from random stochastic processes like genetic drift (Kirk & Freeland, 2011; Luikart et al., 2003; Storz & Nachman, 2003). Gene flow is essential to maintain genetic uniformity between the geographically structured populations. Therefore, migration of

individuals has an immense effect in shaping a pattern of genetic variation observed in a population.

Genetic variation plays a vital role in the trajectory of a population's future viability. This variation refers to the different allelic combinations, also referred as polymorphism, of individual genes. It is because of these different allelic combinations that a population can have a higher adaptive potential. To maintain polymorphism new alleles must be introduced and maintained in populations primarily through migration (Trotter & Spencer, 2008). Variation is fundamentally important because it has been linked to increase fitness, long term adaptability and a deterrence from random genetic drift (Lacy, 1997). This variability both allows a population to have a higher probability of a reduction of inbreeding and increase adaptive potential (Kardos et al., 2021). Migration is one of the central forces that maintains and increases genetic variation because alleles are being exchanged between two populations (gene flow). This provides a homogenizing effect that allows for two population to be genetically similar; however, genetic differentiation can occur when gene flow is limited. Genetic differentiation occurs when migration between populations of the same species is restricted; therefore, gene flow would be limited as well. As a result, subpopulations or geographically structured populations genetic differences can be quantifiable based on their relative genetic frequencies (Gregorius, 1987). This can be caused when occupied habitats or populations are separated by geographic or ecological factors (Pongratz et al., 2002).

Geographical barriers pose a challenge to a species ability to migrate to different populations; therefore, this limits genetic exchange between populations. Gene flow is important because it can increase and maintain genetic variation in a population by introducing new alleles; however, when gene flow is restricted by a barrier there is a possibility for genetic variation in geographical isolated populations to be limited and for genetic drift to occur (Frankel & Soule, 1981; Metcalf et al., 2001; Wright, 1965) . Genetic drift describes an event where random changes in allele frequency are caused by the sampling variation of gametes from generation to generation and is inversely related to the population size (Wright, 1965). Due to the smaller population size this increases the probability of breeding with close relatives therefore decreasing genetic variation and increasing homozygosity, including recessive deleterious alleles. Therefore, an isolated population can have an increased risk of extinction (Frankel & Soule, 1981; Metcalf et al., 2001; Phillipsen & Metcalf, 2009).

Molecular phylogenetics provide the valuable tool to better understand the dynamics that shape geographically structured populations. This field focuses on how genealogical lineages are related to the geographic distribution of populations (Avice, 2004). Phylogenetics estimates the evolutionary change of a genetically related group of individuals by comparing homologous sequences (J. C. Avice & Wollenberg, 1997). To conduct a phylogenetic analysis a suitable DNA region, genetic markers, are identified to reveal evolutionary relationships. In various studies, molecular phylogeography has demonstrated that species

often occur in geographically structured populations, and the members the of populations occupy distinct phylogenetic branches or clades. Therefore, subpopulations that have limited gene flow due to a geographical barrier would demonstrate different branching and clade patterns due to genetic differentiation. As a result, populations can be subdivided into genetically distinct subpopulations (Metcalf et al., 2001; Phillipsen & Metcalf, 2009; Walker & Metcalf, 2008). Under such conditions is where molecular evolutionary biologists can utilize the concept of evolutionary significant units (ESU). This concept correlates population structure and geographic distribution to determine if populations are both isolated and important for conservation; due to the fact that ESU's are historically primary sources of genetic diversity (J. Avise, 2000; Moritz, 1995; Ryder, 1986). However, this criteria is relatively strict and involves congruent signals from both mitochondrial DNA and nuclear DNA. Recently isolated populations may fail these criteria (e.g. not reciprocally monophyletic at mitochondrial and nuclear loci) but may make a unique contribution to biodiversity that should be conserved. Such populations are best characterized as management unit (MU) (Moritz, 1995; Mortiz, 1994). In this study, I investigate the genetic diversity of the cismontane population to the widespread desert populations and in doing so examine their rarity.

Mitochondrial DNA (mtDNA) can be utilized and advantageous to reveal evolutionary relationships in phylogenetic studies. The mitochondria is responsible for the regulation of cellular respiration and therefore generates an

oxidative environment. In vertebrates, mtDNA is a 14-20 Kilobases (kB), circular, maternally inherited molecule that is separate from the nuclear DNA (nDNA) (J. C. Avise et al., 1987). There are various studies that have utilized this tool to elucidate evolutionary patterns in geographically structured populations (Benson, 2006; Lindell et al., 2005; Metcalf et al., 2001; Phillipsen & Metcalf, 2009). Some of the many advantages to using this molecular marker are there is a higher copy number of mtDNA when compared to nuclear DNA. In addition, there is an increased number of genomes replicates per cell division; therefore, there is a high number of copies per cell that are under less selective pressure and subjected to higher mutation probability and less efficient repair mechanisms. Additionally, mitochondrial DNA experiences little to no recombination. Therefore, this maker can be characterized by a rapid rate of evolution (5.29×10^{-9} substitutions per site per year) which generates extensive polymorphism (Avise, 1987). Cytochrome b (1044 base pairs) gene and the ATPase complex (made up of subunit 6 and 8) are mitochondrial gene (866 base pairs) that have been utilized in phylogenetic studies of various species including *Callisaurus draconoides* (Leaché & McGuire, 2006; Lindell et al., 2005). These makers successfully revealed population structure and therefore will be used in this study (Leaché & McGuire, 2006; Lindell et al., 2005).

Introns, non-protein coding nuclear DNA, has been successfully used as a genetic marker to reveal evolutionary relationships in closely related taxa in phylogenetic studies (Greaver, 2019; Leache & McGuire, 2006). Introns are

intervening sequences that are between coding regions called exons in gene that code for proteins. Introns ensure that proper splicing and alternative splicing occur. Since, introns are not under the same selective pressures that are experienced by exons they are an ideal genetic marker because of their natural selection neutrality over much of their sequence. Introns rate of substitution when compared to exons is high and like the mtDNA substitution rate makes them an ideal genetic marker (Thompson, *et al.* 2010). An advantage of nuclear introns and mtDNA genetic markers are that the rate of substitution in intron DNA should match the 3rd base synonymous substitution rate of mtDNA (J. Avise, 2004; Li & Graur, 1991). Unlike uniparental mtDNA, introns are biparentally inherited allowing for the detection of tracking sex-biased migration among subpopulations (Palumbi & Baker, 1994). There is a published study that used the 3rd intron in the nuclear alpha tubulin gene (AT3, 650bp) to reveal the evolutionary relationship of the widely dispersed *C. draconoides* (Larson et al., 2008). The primer set was successful in amplification in *Phrynosoma* and the two closely related species *Holbrookia maculate* and *Cophosaurus texanus* which are all members of the horned lizard, *Phrynosoma* genus (Larson et al., 2008); however, the sequences were not provided and are not GeneBank. In my study AT3 will be tested in its ability to estimate biparental population structure in comparison to population structure estimated by mtDNA molecular makers cytochrome b and ATPase complex. There are other lizard sequences available

in GenBank that will allow us to identify if amplification of this gene was successful.

C. draconoides, the Zebra-tailed lizard, belongs to the *Phrynosomatidae* family of lizards and is a widespread desert lizard found in western North America, Central Mexico, Baja California, Sonora and Sinaloa (Grismer, 2002; Lindell et al., 2005; Pianka & Parker, 1972). This family includes the Earless, Spiny, Tree, Fringed-toed, Side-blotched and Horned lizards (Pianka & Parker, 1972). In California, these species can be found in sandy washes in the San Bernardino basin, Mojave and Colorado Deserts. This species can be characterized by their incredible speed and distinct black and white strip pattern found on the underneath side of their tail (Grismer, 2002). This species can be described as a small to medium sized lizard that has records of adults reaching 109mm (Grismer, 2002). There are 10 subspecies of *Callisaurus draconoides*, and 3 subspecies reside in southern North America: *rhodostictus*, *myurus*, *ventralis* (Adest, 1987; Grismer, 2002; Lindell et al., 2005). *C. d. myurus* range from southern Arizona down toward northern Mexico, whereas *C.d. ventralis* can be observed in northern Nevada. *C.d. rhodostictus* range in between the previous mentioned subspecies ranges in the Colorado (Sonoran) and Mojave Deserts (Grismer, 2002; Lindell et al., 2005). Of great interest there are several populations of Zebra-tailed lizards that reside in the cismontane side of the Transverse and Peninsular ranges in a region known as the San Bernardino basin. This is significant because this San Bernardino basin population of Zebra-

tailed lizards appears to be isolated from their typical desert ranges. The Transverse Mountain ranges of southern California include the San Bernardino, San Gabriel, and Santa Monica Mountains (Schoenherr, 2017). These mountains appear to restrict the cismontane Zebra-tailed lizard populations from the Mojave high desert populations (Fig. 1-4). The Peninsular ranges include San Jacinto, Santa Rosa, as well as Laguna Mountains and appear to restrict the cismontane population from the Colorado low desert populations (Schoenherr, 2017) (Fig. 4). In addition, there are geological passes that separate both the Transverse and Peninsular ranges that potentially could act as corridors of migration to the potentially isolated cismontane population. The Cajon pass extends to the San Bernardino basin to the Mojave Desert; therefore, this pass separates the San Gabriel and San Bernardino mountains (Schoenherr, 2017)(Fig. 2). It is important to note that this pass is where the San Andreas and San Jacinto faults are approximately 2 miles apart (Schoenherr, 2017). The Banning pass separates the San Jacinto mountains of the Peninsular and the San Bernardino Mountains of the Transverse Ranges (Fig. 3) (Schoenherr, 2017). Therefore, this pass extends from the Colorado low desert to the cismontane population. These mountains ranges and geological passes are significant because there is potential for cismontane populations of *C. draconoides* to be isolated with limited opportunities for dispersal into their natural ranges.

San Bernardino basin was formed as recently as 1.5 million years ago (mA) due to a geological event that caused a potential barrier to form between

the cismontane and the deserts (Matti & Morton, 1993). Prior to this event there was connectivity from Colorado to Mojave Desert. A strike-slip movement toward the Coachella Valley segment was experienced by the San Andreas fault to the San Jacinto fault accelerating a shift (Matti & Morton, 1993; Schoenherr, 2017). This movement produced two results that completely shifted southern California's geographic structure. First, this movement caused the San Gorgonio, also known as Banning Pass, to experience a northwestern uplift (Matti & Morton, 1993; Schoenherr, 2017). Secondly, this movement resulted in the San Bernardino and San Jacinto Mountain blocks to experience an accelerated thrust causing the ranges to uplift during the Miocene era (Matti & Morton, 1993; Schoenherr, 2017). This geological event caused the cismontane region to develop for the past 750,000 years at a lower elevation and a Mediterranean habitat to emerge (Matti & Morton, 1993; Schoenherr, 2017).

The emergence of this Mediterranean habitat produced a discordance of preferable habitat for the cismontane *C. draconoides*. This habitat does not resemble their natural desert habitat that is observed in the Mojave and Colorado Desert ranges. The Mediterranean habitat is characterized moderate winter precipitation and hot summers (Schoenherr, 2017). In contrast the Mojave (high) and Colorado (low) deserts can be characterized by their low precipitation environment (Schoenherr, 2017). Additionally, deserts experienced wider temperature ranges throughout the year. On average a desert annual temperature range is 50 degrees Fahrenheit and Colorado desert have an annual 130

degrees Fahrenheit range (Schoenherr, 2017). This is an immense contrast to the 32 degrees Fahrenheit annual range experienced in the cismontane habitat(Schoenherr, 2017). The evolution of the cismontane habitat and separation from the deserts could have had an immense generational effect on the population structure seen in this species in this newly emerged Mediterranean habitat.

The cismontane population's potential for isolation presents an exemplary source to study phylogeography. The molecular information available focuses on mitochondrial DNA and allozyme data; however, there is limited published nuclear DNA sequence, such as introns (Larson et al., 2008; Leaché & McGuire, 2006). There are discrepancies in between what mitochondrial data verses allozyme data suggests about potential or limited potential of gene flow between populations of *C. draconoides* or *Phrynosoma* (Adest, 1987; Leaché & McGuire, 2006; Lindell et al., 2005). One study in Baja California demonstrated that mtDNA data (cyt.b and ATPase) show deep genealogical divergence patterns this suggesting there was a large genetic differentiation between isolated populations; whereas allozyme data demonstrates high allozyme similarities suggesting low genetic differentiation among the same populations (Adest, 1987; Lindell et al., 2005). The explanation for this result was not clear; however, the uniparental inheritance of mtDNA and the possibility for lack of neutrality in biparental allozyme may be a feasible explanation (Parker et al., 1998). Although the mtDNA and allozyme data were not in congruence with one another

in the studies mentioned, adding nuclear DNA sequence data could possibly elucidate historical relationships.

The goal of this study is to do a thorough population genetic analysis of cismontane *C. draconoides* in comparison to populations that reside in the Mojave high and Colorado low deserts. This is important because the Transverse and Peninsular Mountain ranges with the uplift of the Cajon and Banning pass and subsidence of the San Bernardino Valley basin appear to have isolated the cismontane population from their typical desert range with limited opportunity for dispersal. Mitochondrial sequence (cytochrome b and ATPase) and nuclear intron sequence (AT3) were utilized in this comparative genetic analysis. First, mitochondrial, and nuclear sequence were used to determine if there are lineage breaks that are consistent with geographic region. Second, mitochondrial, and nuclear sequence are used to determine if the Cajon and Banning pass serve as historical migration corridors to the cismontane locations.

Specific Aims

The broad goal of this project is to study the population genetic composition of the San Bernardino basin cismontane Zebra-tailed lizards, *C. draconoides* that reside within the alluvial fan drainages southwest of the Transverse Mountain ranges and the northwestern of the Peninsular Mountain ranges; as well as compare them to populations in the Mojave and Colorado deserts of southern California. The individuals within the cismontane location are intriguing for two reasons. First, they are the only known coastal population in California. Second, mountain ranges appear to pose a geographic barrier to dispersal, therefore limiting the ability for populations to exchange migrants with populations residing in Colorado and Mojave Desert. A more specific aim of the study is to understand how the mountain ranges and passes between them may have influenced the genetic structure of *C. draconoides* within the cismontane sampling locations in comparison to individuals that reside in the Mojave and Colorado desert. This project analyzes how (or if) the Cajon Pass to the north and Banning Pass to the west, may have served as migration corridors to the cismontane locations (Fig. 1-4). To measure the genetic composition of the desert and cismontane populations this study will utilize uniparental mitochondrial (mtDNA) and biparental nuclear (nDNA) as genetic markers. These genetic markers allowed me to both reconstruct phylogenetic relationships and to generate population genetic models to better understand how the mountain ranges and passes have structured these populations. Phylogenetic

reconstruction employed was Bayesian, maximum likelihood, and distance-based approaches to examine the congruence among the analyses. I used AMOVA and GenALex to analyze the molecular variance and population structure, including F-statistics analogues and migration rates among geographic regions (Peakall & Smouse, 2012; Tamura et al., 2021). Isolation by Distance model (IBD) was examined by a Mantel test (Mantel, 1967). Our final goal of this study is to see if the cismontane populations comprise an evolutionary significant unit (ESU) and to propose conservation measures to preserve the *C. draconoides* cismontane habitat (Moritz, 1995)

CHAPTER TWO

MATERIALS AND METHODS

Sampling and Sequence Analysis

The fifty-eight individuals were collected and accessioned from thirteen different sampling locations across the range of *C. draconoides* in southern California and Nevada by the San Bernardino County Museum (SBCM). There are 1-10 individuals from each sampling location that were tested in this study (Table 1). The sampling locations are separated primarily by the Transverse and Peninsular ranges, extending from the cismontane region to the Mojave and Colorado desert regions (Fig. 1). In addition, 3 individuals were used from the Nevada region of the Mojave desert and were organized in their own region because the distance between populations was immense (Fig.1). There are two types of tissues that were used for DNA extractions: liver tissue (n=56) and testes (n=2). The samples were stored in the liquid nitrogen tank until extractions were ready to be conducted. The outgroup mitochondrial sequences included were obtained from GenBank (Lindell et al., 2005) (Table 9). Since our outgroups is more distantly related this addition allows for the analysis to have more confidence in the relationships formed during the phylogenetic analyses.

This research used two methods for DNA extractions: first, approximately 0.60-0.85grams of liver tissue were used for a phenol-chloroform extraction method and a Qiagen DNeasy Tissue kit method used 10-20 milligrams of liver

tissue. Once extractions were completed samples were stored at -20°C. A 1027 base pair cytochrome b gene was amplified via PCR. The thermal cycling parameters for PCR were initial denaturation at 94°C for 5 minutes followed by 40 cycles of: denaturation at 94°C for 30 seconds, annealing at 62°C for 1 minute, extension at 72°C for 2 minutes and after the cycles were complete there was a final extension at 72°C for 10 minutes. The alpha-tubulin (AT3) intron gene thermal cycling parameters for PCR were initial denaturation at 94°C for 5 minutes followed by 35 cycles of: denaturation at 94°C for 1 minute, annealing at 50.7°C for 30 seconds, extension at 72°C for 1 minutes and after the cycles were complete there was a final extension at 72°C for 1 minute. The ATPase mtDNA follows the same thermal cycling parameters for PCR as the AT3 intron gene. The reaction mixture for each sample was 1ul of each primer, 1ul of genomic DNA, 22ul of deionized water and 25 ul of a 2x PCR mater mix that includes the 0.05U/ul Taq DNA polymerase, reaction buffer, 4mM MgCl₂, and 0.4mM of each dNTP. A 0.8% agarose gel was used to visualize the PCR products via gel electrophoresis. PCR product base pair length was approximated based on Thermo Scientific GeneRuler 50bp DNA Ladder; therefore, both band size and relative intensity was recorded. Before sending the samples off to be sequenced (cytochrome b, Laragen; ATPase and AT3 intron, Psomagen) the PCR products were purified using the ExoSAP-IT kit (Amersham Pharmcia Biotech).

The cytochrome b and Adenosine triphosphatase (ATPase) mitochondrial sequences heavy and light strand were assembled in via de novo assemble

plugin available in the software package Geneious (Geneious Prime 2019.1.3 (<https://www.geneious.com>)). In addition, sequences were proofread and aligned using the multiple pairwise alignment (MUSCLE) available in Geneious (Geneious Prime 2019.1.3 (<https://www.geneious.com>)). This alignment allowed me to verify that both mtDNA was in reading and was indeed coding sequence. As a quality control check sequences were subjected to a NCBI BLAST and compared to the coding regions of Zebra-tailed lizards in Lindell project (Peakall & Smouse, 2012). Both mitochondrial sequences were checked for variable sites and conserved regions were determined with GenAEx software package (Peakall & Smouse, 2012). Haplotypes were assembled for both molecular markers. The nucleotide base ratio, transition vs transversion ratio, non-synonymous vs synonymous site ratio and amino acid variable sites were determined using MEGA (Tamura et al., 2021). Then, aligned sequences of cytochrome b and ATPase were translated into amino acids to check for pseudogenes (NUMTS). The translated amino acids were able to determine the 1st, 2nd and 3rd codon variable sites. After separate analyses, mitochondrial molecular markers were concatenated and then subjected to the same analyses together.

Alpha-Tubulin 3 (AT3) intron was employed as a nuclear marker used to compare to the mtDNA. AT3 nuclear intron sequences were proofread and aligned using the multiple pairwise alignment (MUSCLE) available in Geneious (Geneious Prime 2019.1.3 (<https://www.geneious.com>)). In addition, polymerase

chain primers were edited out of the sequence when the exon-intron boundaries were determined. Exon-intron boundaries were detected by the *Sceloporus* mRNA model (Westfall et al., 2020). The *Sceloporus* mRNA model allowed for a sequence comparison to be made between nuclear intron sequence in this project and known annotated mRNA sequence (Westfall et al., 2020). By using this comparison and known sequence that is an indication of the exon-intron boundary the nuclear DNA was properly trimmed to only include the intron sequence. Nuclear haplotypes were not constructed for this molecular marker due to lack of variation of the gene among all individuals. Individuals from all populations were sampled to see if intron variation was present. No intron sequence variation was observed (n=38) in a subset of preliminary data. Therefore, no nucleotide base ratio, transition vs transversion ratio, non-synonymous vs synonymous ratio and amino acid variable sites were determined since there was no nuclear variation observed. Identically, sequences were aligned and subjected to a NCBI BLAST to ensure that the desired gene was indeed amplified.

Phylogenetic Inference

Phylogenetic analysis of *C. draconoides* cytochrome b, ATPase and concatenated mtDNA haplotypes were estimated using Geneious for Maximum Likelihood (ML), Neighbor-joining (NJ) and Bayesian analysis (BA) (Geneious Prime 2019.1.3 (<https://www.geneious.com>)). The HKY85 model was selected for the best fit model of evolution using the maximum likelihood test (BIC score) in MEGA. This model was used for the ML, NJ and BA for both mtDNA genes of interest. The node support for ML and NJ was estimated using non-parametric bootstrapping in Geneious (Geneious Prime 2019.1.3 (<https://www.geneious.com>)). The Bayesian analysis was performed for cytochrome b, ATPase and the concatenated mtDNA sequences using the following parameters: random starting tree, trees were sampled from the posterior distribution every 1,000 generations for 3,000,000 generations using four Markov Chain Monte Carlo (MCMC). After Burn-in leveling every 3,000 trees were discarded. The phylogenetic trees were rooted using, *Holbrookia lacerate* (Roelke et al., 2018) and two subspecies of *C. draconoides* (Lindell, 2004). Since nuclear intron AT3 sequences lacked variation no phylogenetic inference was conducted.

Population Genetics

In order to test our hypotheses and to understand the hierarchical partitioning of genetic variation between the cismontane and desert populations of *C. draconoides* of southern California we tested two geographic population structure models by analysis of molecular variance (AMOVA) (Excoffier et al., 1992) of cytochrome b, ATPase and concatenated sequence data using GenAlEx (Peakall & Smouse, 2012). For some models, sampling locations were grouped based on their cismontane, Mojave desert (high) and Colorado desert (low) geographic regions. In other models, individuals were grouped based on their sampling locations. Genetic distances were determined using Nei's distance method (Nei, 1987). The cytochrome b and ATPase genetic distances were determined and utilized in AMOVA, ϕ -statistics (F_{ST}), migration rate (N_m), principal coordinate analysis (PCoA), and Mantel tests (Peakall & Smouse, 2012). ϕ -statistics were calculated for each population and geographic region that correlated with that population. ϕ -statistics and variance were evaluated using 999 permutations of sequences among the populations (Peakall & Smouse, 2012). This statistic reveals whether genetic difference seen is significant in population structure. Restricted gene flow should be detectable when analyzing the ϕ scores obtained from AMOVA. Mantel tests were performed to look for an association between genetic variation and geographic distance to examine isolation

by distance (IBD) model (Peakall & Smouse, 2012). Mantel tests were conducted to test whether the population structure seen could be explained by isolation by distance (IBD). In this study six Mantel tests were performed at a regional level utilizing ϕ_{PT} distance indices of California and Nevada samples (Figs 30-35).

CHAPTER THREE

RESULTS

Sampling and Sequence Analysis

There were 1140 base pairs that were successfully sequenced for cytochrome b mtDNA in all 58 individuals used in this study (Table 1). The base composition was 32.1% adenine, 29.7% thymine, 26.2% cytosine and 12% were guanine bases (Table 10). The transition ratio was 0.87 and transversion ratio was 0.14. There were 112 variable sites across all the *C. draconoides* individual mtDNA sequence. There was no data missing in the sequences. There were 13 variable amino acid sites when the cytochrome b sequence was translated to amino acid sequence. Approximately 83% of the variable sites were at the 3rd codon position, 14% were at the 1st codon position and 3% were at the 2nd codon position. Each individual sequence was organized into 36 haplotypes based on similarity in nucleotide variable sites. The number of *C. draconoides* individuals in each haplotype ranged from 1-4 lizards. All haplotypes were restricted to their geographic regions excluding the two populations that reside in the Cajon Pass and Banning Pass (Fig 2-3) (Table 4). Individuals from Verdemont, Kenwood and Muscoy, representing populations from the cismontane geographical region, share 3 of the the 8 cismontane haplotypes (Table 4).

In the ATPase complex 820 base pairs were successfully sequenced for 55 individuals used in the study (Table 2 and 10). Muscoy 3575, Jawbone 3581 and Snow Creek 3503 were not successfully sequenced; therefore, they were not

included in the ATPase and concatenated sequence analyses. The base composition for this gene was the following: 35% (A), 24.6% (C), 10.4% (G), and 29.3% (T) (Table 10). The transition ratio was equal to 0.726 and transversion ratio was 0.236. There was 69 variable mitochondrial nucleotide sites and 18 variable amino acid sites observed when mitochondrial DNA was translated into amino acids. There were 91.5% of identical sites and a pairwise identity of 98.6% (Table 10). In the overall ATPase complex, there was 18 variable amino acid sites. Approximately, 59% of the substitutions were at the 3rd codon position, 30% were at the 1st codon position and 10% were at the 2nd codon position. The 55 individuals that were amplified were organized into 37 haplotypes. Individuals per haplotype ranged from 1-9 and all but two of the haplotypes had individuals within the three geographic regions (Table 5). There were exceptions to this instance with haplotypes 25 and 36, both haplotypes contained admixture of a pass population sharing a haplotype with individuals from the Mojave Desert and Cismontane (Table 5).

The concatenated cytochrome b and ATPase sequences consisted of 1,960 bp for 55 individuals. There was 1,402 bp (71.5%) of identical sites and a pairwise identity of 97%. Base frequencies were the following: 33.6% (A), 25% (C), 11.3% (G) and 29.5% (T) (Table 10). Together the concatenated sequence had 31 variable amino acid sites. Approximately, 75% of the substitutions were at the 3rd codon position, 20% were at the 1st codon position and 5% were at the 2nd codon position. The transition (Ti) ratio was 0.871 and transversion (Tv) ratio was

0.128 (Table 11). Concatenated mtDNA sequences were then organized into 47 haplotypes (Table 6). These haplotypes were made up of individuals from the same sampling location and geographic region; apart from haplotype 37 which consists of one Kenwood and Verdemont individuals both representing the cismontane region (Table 6). All mtDNA and nuclear molecular markers were NCBI BLAST® to ensure the correct gene had been isolated.

The alpha-tubulin (AT3) 538 bp were successfully sequenced for the 35 individual subsets sent out. When the sequence was analyzed, it was observed that 534 were identical and the pairwise identity was 99.8%(Table 10). The base distribution was the following: 32.7% (A), 18.9% (C), 19.2% (G), and 29.3% (T) (Table. 10). Due to the lack of variation no haplotype construction, transition vs transversion ratio, non-synonymous vs synonymous ratio and amino acid variable sites were determined. Sequences were aligned and subjected to a NCBI BLAST to ensure that the desired gene was indeed amplified and trimmed to only include the intron.

Phylogenetic Inference

Phylogenetic methods revealed that each analysis formed three well-supported clades for the cytochrome b sequence (98-100%) (Fig. 5). Tree

topologies were congruent in the Bayesian, Maximum Likelihood, Neighbor-Joining Haplotype analyses. In all three phylogenetic analyses Clade A demonstrated Mojave desert and Colorado desert admixture. Clade B consisted solely of Mojave desert individuals. Clade C consisted of Phelan, Snow Creek and cismontane individuals. When examining each clade's geographic structure, Clade A consists of individuals that reside southeast of the Peninsular Mountain ranges in the Colorado low desert and several individuals that reside northeast of the Transverse Mountain ranges in the Mojave high Desert. This clade consisted of majority of the Colorado low desert populations except for 5 Phelan pass individuals and 1 Pioneertown Mojave Desert individual. Geographically Clade B consist of only individuals that reside in the Mojave Desert northeast of the Transverse Mountain ranges. Clade C consist of a mixture between pass and cismontane populations (Fig.5). These cismontane individuals represent the southwest of the Transverse Mountain ranges and the northwestern of the Peninsular Mountain ranges.

The Bayesian and Neighbor-Joining phylogenetic analysis of ATPase formed two well-supported clades (83-100%). Whereas, in the Maximum Likelihood analysis demonstrated lower bootstrap values for the same two congruent clades formed in the Bayesian and Neighbor-Joining analyses. All three analyses can split into two clades, A and B. In all three phylogenetic assessments clade A demonstrates all Colorado Desert region individuals with admixture of the Mojave Desert individuals (Fig. 6-8). In clade B it can be

observed that there is an admixture of Cismontane, Mojave Desert and Colorado Desert individuals in all three analyses. It important to note that in this clade the only Colorado Desert individuals seen in this clade are Snow Creek individuals which reside at the Banning Pass (Fig. 6-8). In both the Bayesian and Neighbor-Joining phylogenetic analyses there is multiple polytomy lineages seen within clade B.

The concatenated mtDNA phylogenetic assessments observed three well supported clades (82.5-100%) and tree topologies were congruent with previous analyses. In clade A there is admixture of Colorado Desert and Mojave Desert individuals. Majority of the Mojave Desert individuals in this clade are the Phelan Mojave desert pass individuals apart from one Pioneer Town individual. Whereas clade B consists of only Mojave Desert individuals and is absent of any individuals from the Phelan Mojave Desert pass location. In clade C there is an admixture of Cismontane, Colorado and Mojave Desert individuals; however, the only desert individuals seen are the Cajon and Banning pass individuals (Fig. 9-11).

Population Genetics

To examine geographic population structure, we organized the following models: (1) all the sampling populations and (2) each population grouped in their

geographical region (Cismontane, Mojave Desert, Colorado Desert and Nevada). Both models showed significant geographic structure (Figure 11-18). The level of migration (N_m) was similar in both model, $N_m > 0$. This was seen in comparing the ϕ_{PT} scores and N_m scores for cytochrome b, ATPase, and concatenated sequences (Fig. 12-20). When looking at AMOVA scores for all the California and Nevada sampling populations the following was ranges observed for cytochrome b, ATPase, and concatenated sequences: $\phi_{PT} = 0.350-0.405$, $P=0.001-0.003$ and $N_m = 0.735-0.928$ (Fig. 12-20). When each population was grouped into their geographic region the following ranges observed for cytochrome b, ATPase, and concatenated sequences: $\phi_{PT} = 0.276-0.307$, $P=0.001-0.003$ and $N_m = 1.130-1.314$. When the geographically isolated Nevada samples were removed from the California Mojave Desert the population structure values remain similar ($\phi_{PT} = 0.178-0.208$, $P=0.001-0.003$ and $N_m = 1.90-2.313$).

To visualize any patterns in genetic relationships among sampling and geographic regions principal coordinates analyses (PCoA) were performed to observe if genetically distinct populations clustered in accordance with their geographic region. All PCoA analyses visualize and correlation between genetic structure and geographic location (Fig.20-29).

Mantel tested showed no significant relationships among geographic distance and genetic structure, suggesting that other factors may play a role (Fig. 30-35).

CHAPTER FOUR

DISCUSSION

Overview

I have demonstrated that the isolated cismontane population of Zebra-tailed lizards are unique due to their phylogenetic and population genetic structure. Cytochrome b, ATPase and concatenated sequences demonstrated significant sequence divergence from desert populations, whereas the nuclear DNA did not. This reinforces the hypothesis that this isolation was caused by recent (<750,000 ya) tectonic plate events that have resulted in currently no or very limited migration between the cismontane and desert regions (Matti & Morton, 1993) .Therefore, the cismontane population is now isolated in the unique and limited alluvial sage scrub habitat in the San Bernardino Basin. As a result, I argue that the cismontane population of Zebra-tailed lizards constitutes a management unit and deserves immediate attention in conservation efforts.

Phylogeography

To further support the population structure observed in the genetic model's cytochrome b, ATPase and concatenated haplotype sequences were subjected to Bayesian, Maximum Likelihood, and Neighbor-Joining analyses. In every analysis clade A was made up of Colorado Desert individuals and with

Mojave Desert pass individuals (Fig 5-10). In cytochrome b and concatenated analysis 3 clades were formed; in every result clade B was made up of only Mojave Desert individuals and clade C contained Cismontane, Cajon pass and Banning pass population admixture (Fig. 5, 8,9, 10). Clade C contained no Mojave or Colorado desert individuals. Clade C suggests it is highly likely that the passes populated the cismontane region in the San Bernardino basin. In the ATPase phylogenetic analyses two clades were formed, clade A and clade B. Clade B contains admixture of Cismontane, Mojave and Colorado desert pass population (Fig. 6-7). The more unresolved branching demonstrates a similar overall grouping to cytochrome b and concatenated sequences. These results, including the identical intron sequence data, leads us to hypothesize that the population structure that is observed is due to a recent geological separation event restricting gene flow between the desert and cismontane populations.

Population Genetics

The population structure supports the hypothesis of the cismontane populations characterized by restricted gene flow through the passes to the deserts. The mtDNA was strongly supported by the numerous genetic analyses performed in this study when organized in population genetic models. The patterns that are hypothesized is a result of geographic isolation that cause the population to have high genetic differentiation patterns (Φ_{PT}). Analysis of

molecular variance (AMOVA) for this study are significant regional ϕ_{PT} scores that ranged from 0.276-0.307 with a migration (N_m) rate that ranged from 1.130-1.197 (Fig. 11-16). The principal coordinate analyses (PCoA) results bolster the structure observed in the AMOVA analyses (Appendix A, Fig. 20-29). The grouping observed illustrates that Cismontane is genetically the least similar to the Colorado desert region (Low Desert), whereas Mojave Desert is consistently in the between the Colorado Desert and Cismontane clusters indicating that is a higher degree of similarity to either region (Appendix A, Fig. 20-29). It is a possibility the Mojave Desert may have contributed more to the cismontane region before geneflow was restricted. This is congruent with the phylogenetic analyses described above.

To determine if the population structure observed in this study was correlated with isolation by distance (IBD), Mantel tests were conducted. For example, large genetic differentiation in a population could correlate to a large physical distance between them (Wright, 1942). In our case the Mantel tests level all six Mantel tests, including California and Nevada samples, produced a negative value; suggesting no association between the population structure observed and geographic distance (Figs 30-35). This suggests that topographic features play an important role in the structure of cismontane region. I will develop this hypothesis below.

History of Connectivity and Habitat

The San Bernardino basin, where the Zebra-tailed lizards reside, was formed due to an accelerated geological event (eruption of the San Jacinto fault) that occurred approximately 1.5 mA ago (Matti & Morton, 1993) .Before this event the San Bernardino basin consisted of an elevated alluvial fan that stretched from the passes to northwestern riverside county (Matti & Morton, 1993) .During this time there was contiguous habitat suitable for Zebra-tailed lizards. As a consequence of the formation of the San Jacinto fault the San Bernardino Basin was formed and has evolved at a different elevation than in both deserts for the past 750,00 years (Matti & Morton, 1993; Schoenherr, 2017). I hypothesize the possible dispersal corridor used by this species had been interrupted and contiguous migration movement between Cismontane, Mojave and Colorado Desert became restricted. This isolation of the cismontane populations is reflective in both the phylogeographic structure, and the population genetic structure used in this study.

Currently, the San Bernardino Basin or cismontane region can be characterized as a Mediterranean habitat. As a result, this ecology differs from that seen in the Mojave and Colorado deserts. A Mediterranean climate can be described by hot summers and moderate winter precipitation; whereas the Colorado and Mojave deserts can be characterized as low precipitation, temperature extremes, windy, high light intensity, and nutrient poor soils (Schoenherr, 2017). Both of the deserts are characterized by their sandy

washes, which is prime habitat for *C. draconoides*, and creosote bush that grow abundantly due to the high alkaline soils. (Schoenherr, 2017). These sandy washes present in only isolated patches in all cismontane locations used in this study. Consequently, this species' preferred habitat through the Banning and Cajon passes, at best, is dispersed into steppingstones or islands. Both of these dispersal models could elucidate the evolutionary history of the cismontane population structure we see presently.

Models of Partition

The dispersal models under investigation in this study are attributed to the physical dispersal of sampling locations, phylogenetic organization and population structure elucidated by the sequence analysis. One model that was considered to explain causation of the population structure observed is the isolation by distance (IBD) often utilized in an island model of population structure. This model assumes, that genetic differentiation accumulates with distance under the assumption that migration to subpopulations has been restricted (MacArthur & Wilson, 1963; Van Strien et al., 2015; Wright, 1965). According to the results of our Mantel tests the data reveal that the association between geographic and genetic distance is not significance. As a result, the IBD model is not the explanation for the structure that is observed.

The steppingstone model address the discontinuity or limited ability for an individual population to migrate over a vast geographic range by migrating only to adjacent or nearby subpopulations per generation (Kimura & Weiss, 1964). This model hypothesizes that a population's genetic variation is dependent on (1) the number dimensions that present an obstacle for migrants to travel to other subpopulations (2) and the number migrants each generation that successfully migrant to the neighboring colonies (Kimura & Weiss, 1964). It is important to note that each subpopulation is susceptible to genetic drift, mutation, and short-range migration (Kimura & Weiss, 1964). In previous research this model has illustrated that first-diverging lizard lineages demonstrated higher genetic divergence due to their longer period of being isolated (Lin et al., 2002; Yang et al., 2018). This study demonstrated that geological events created potential isolation and migration discontinuity (Lin et al., 2002; Yang et al., 2018). One observation that questions whether this spatial model best explains the population structure observed in this study is, that were no intervening populations observed within the pass corridors and desert regions during specimen collection (Per communication Gerald Braden San Bernardino County Museum). Such sites would be crucial for *C. draconoides* migrants to travel from one geographic region to the other. In a previous capture and recapture study researchers found that *C. draconoides* return and remain in their home ranges; as a result the average home range was approximately 4.6m² (Frost & Bergmann, 2012; Tanner & Krogh, 1975). This evidence suggests it would be

difficult for the species migrate over great distances to other geographic regions over many generations. I conclude that before the geological events of 1.5 mA a stepping migration corridor existed between the cismontane and desert regions. Over the last 750,000 that connection has disappeared resulting in the current divergence of the cismontane region from the desert population of Zebra-tailed lizards.

Closing Remarks

I hypothesis that prior to the development of the San Jacinto fault and the subsidence of the San Bernardino basin there were less geographic barriers to migration from cismontane California to the Colorado and Mojave deserts. The local regional patterns of genetic differentiation we see today are the result of these large-scale tectonic events. Cytochrome b, ATPase and Concatenated mitochondrial DNA demonstrated that genealogical breaks that correlate to these geographic regions (Fig. 5-10). The principal coordinate analysis (PCoA) results were in congruence with these findings (Fig. 20-29). Due to the admixture observed in Clade A and Clade C in the phylogenetic analyses, the data suggests that Banning (Colorado Desert) and Cajon (Mojave Desert) passes no longer or rarely allow migration between the desert geographic regions into the cismontane populations. Mantel test results characterized that genetic structure is not associated with distance. Therefore, mountain range, pass topology and

steppingstone spatial models best explain the structure currently observed. In addition, identical intron sequence data elucidated that San Bernardino basin isolation is recent and in agreement with the geologic data.

I argue that the cismontane population of Zebra-tailed lizards constitutes a management unit (MU) deserving immediate conservation efforts for the following reasons: (1) significant mitochondrial phylogenetic and population genetic structure yet there is no nuclear DNA divergence from desert populations, (2) the cismontane populations reside in a unique alluvial habitat type and (3) these small, isolated populations are a part of a rapidly vanishing alluvial scrub habitat.

APPENDIX A

FIGURES

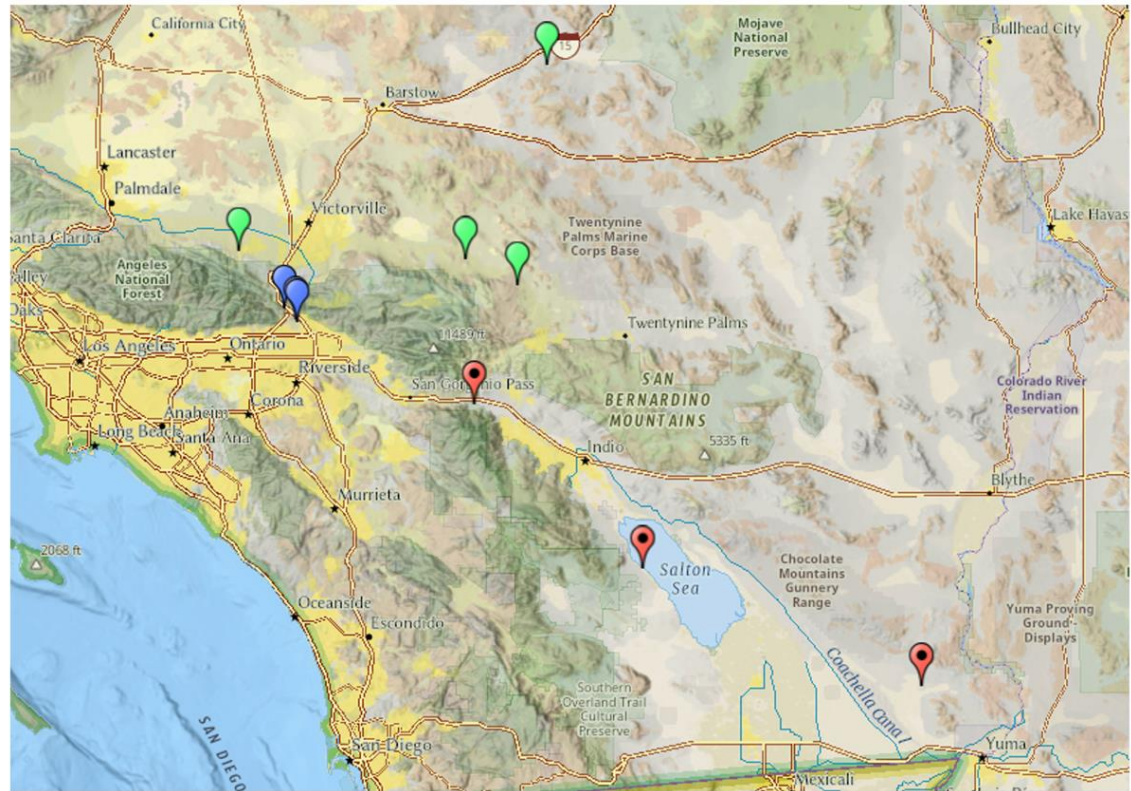


Figure 1. This is a map of all sampling locations utilized in this study in both California and Nevada. Green pins represent Mojave Desert locations, Blue represent cismontane locations, and Red represent Colorado Desert locations.

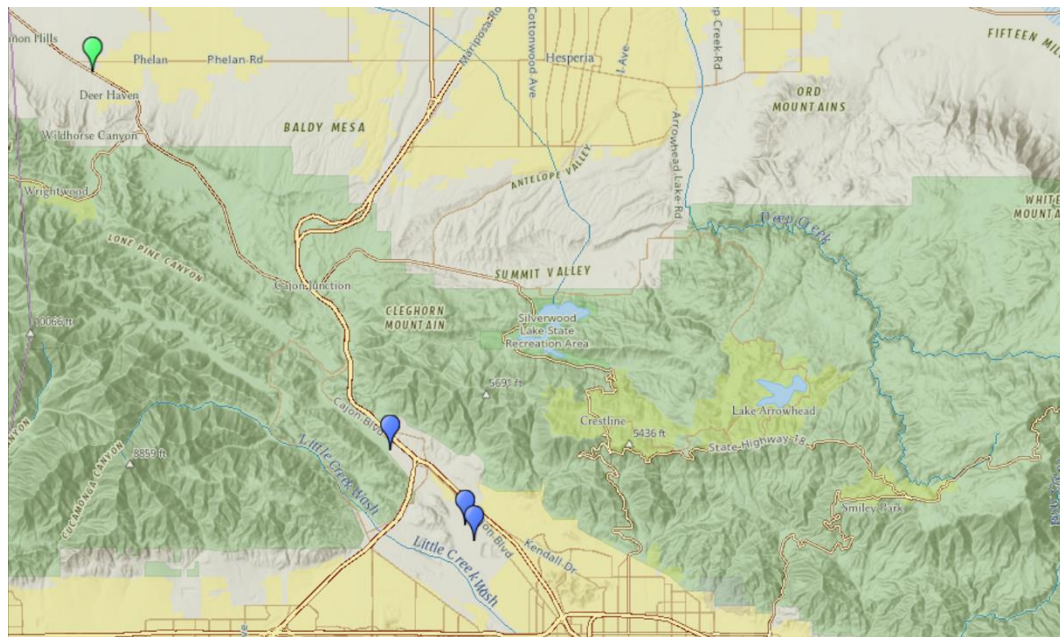


Figure 2. Cajon pass region that is between the San Gabriel and San Bernardino mountains which could act like a corridor between Mojave Desert and Cismontane. Blue Pins represent Cismontane and Green pin represents the Phelan sampling location in Mojave Desert.

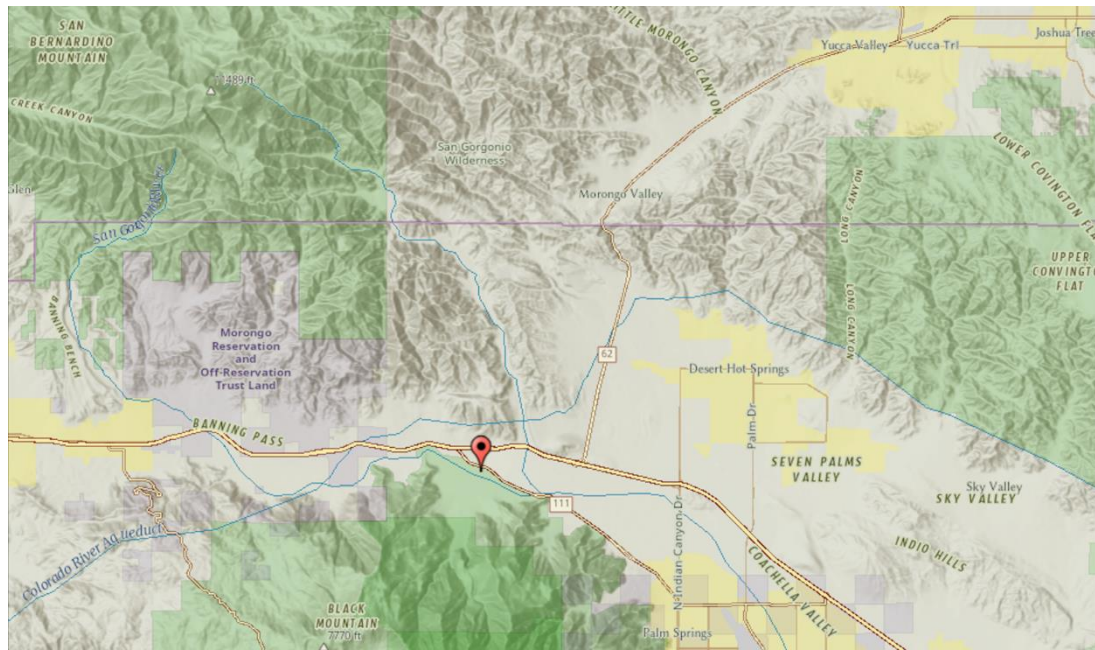


Figure 3. Banning pass region that is between the San Jacinto and San Bernardino mountains which could act like a corridor between the Colorado Desert and Cismontane. Red pins represent the Snow creek sampling location in Colorado Desert.

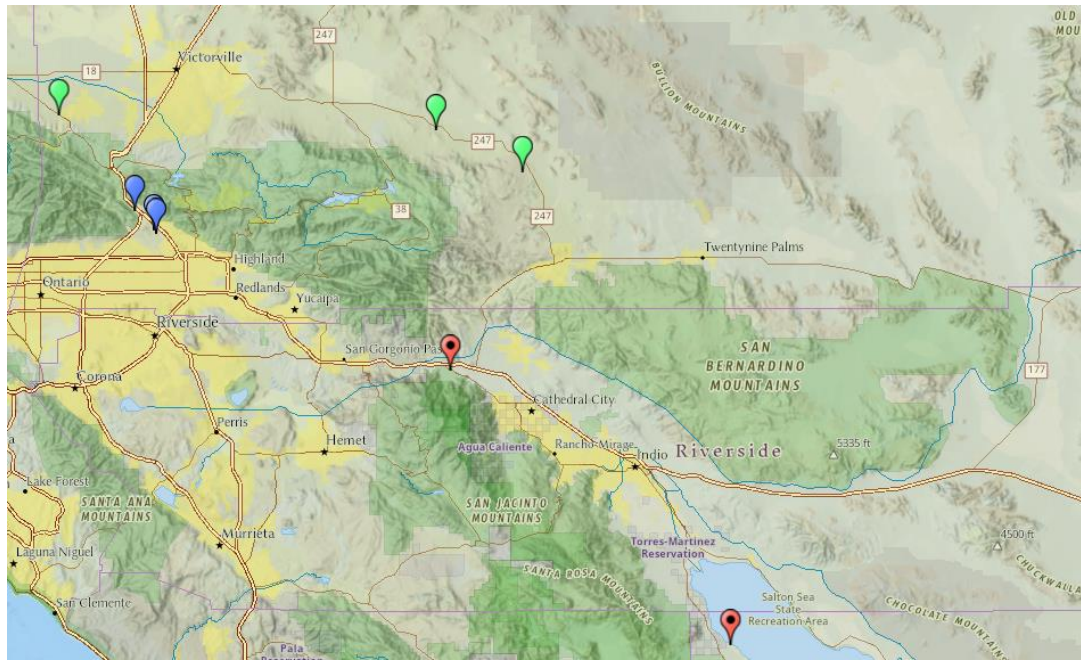


Figure 4. California map of the Transverse and Peninsular Ranges used in this study are shown.

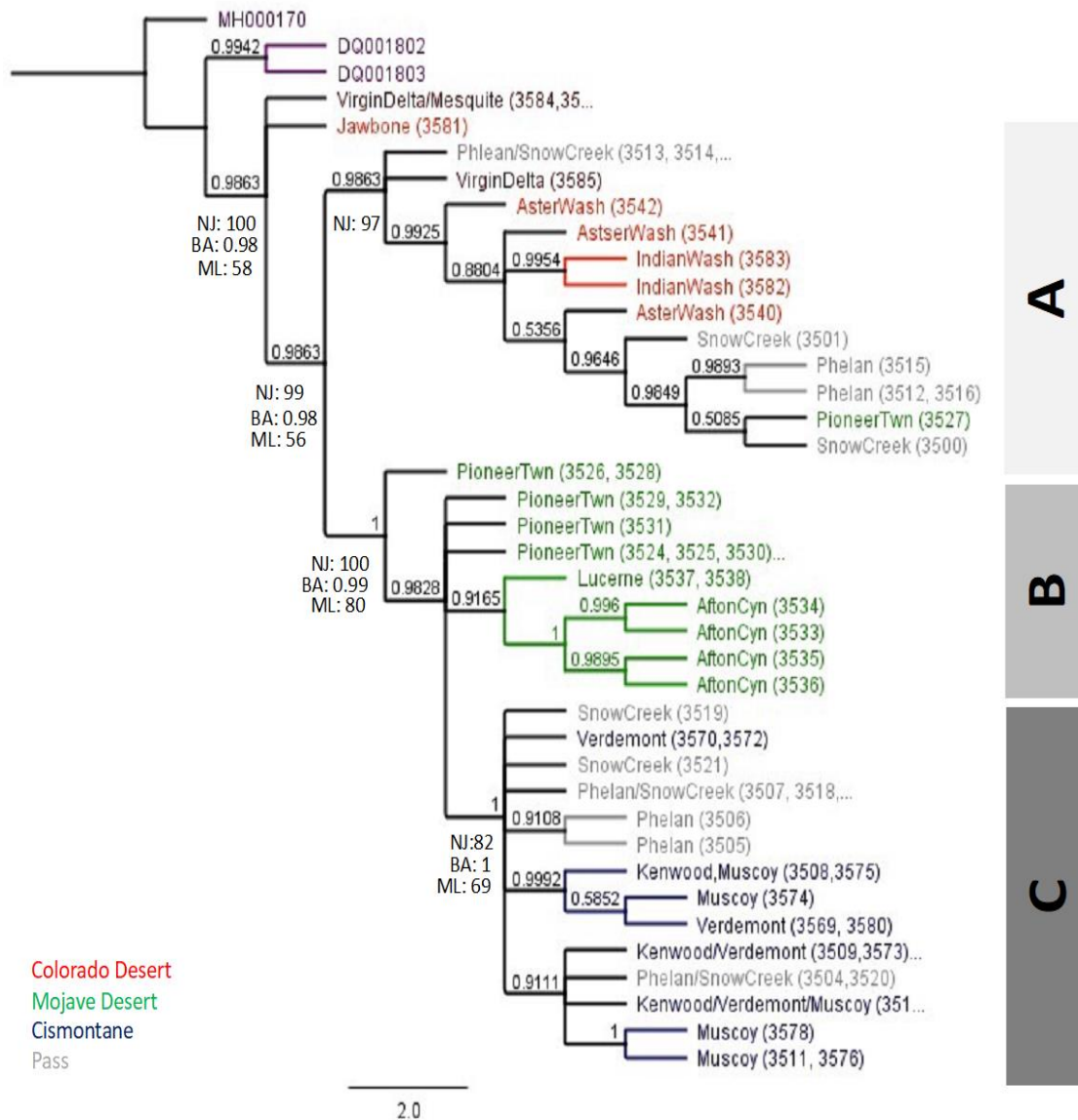


Figure 5. A Bayesian phylogenetic tree based on cytochrome b haplotype sequence. HKY85 genetic model used on the 37 haplotypes samples. The following were outgroups: Virgin Delta (NV), Mesquite (NV), MH000170 (Roelke and et.al, 2017), DQ001802 and DQ001803 (Lindell and et.al, 2005). MH000170 is a *Holbrookia lacerate* individual used to root the phylogenetic tree. DQ001802 is a *Callisaurus brevipes* and DQ001803 is a *Callisaurus bogerti* (Lindell et al., 2005). Neighbor-joining (NJ), Bayesian (BA), and Maximum likelihood (ML) support values are included. Clade A includes Colorado Desert and Phelan individuals. Clade B only has Mojave Desert individuals. Clade C has cismontane, Cajon and Banning pass individuals

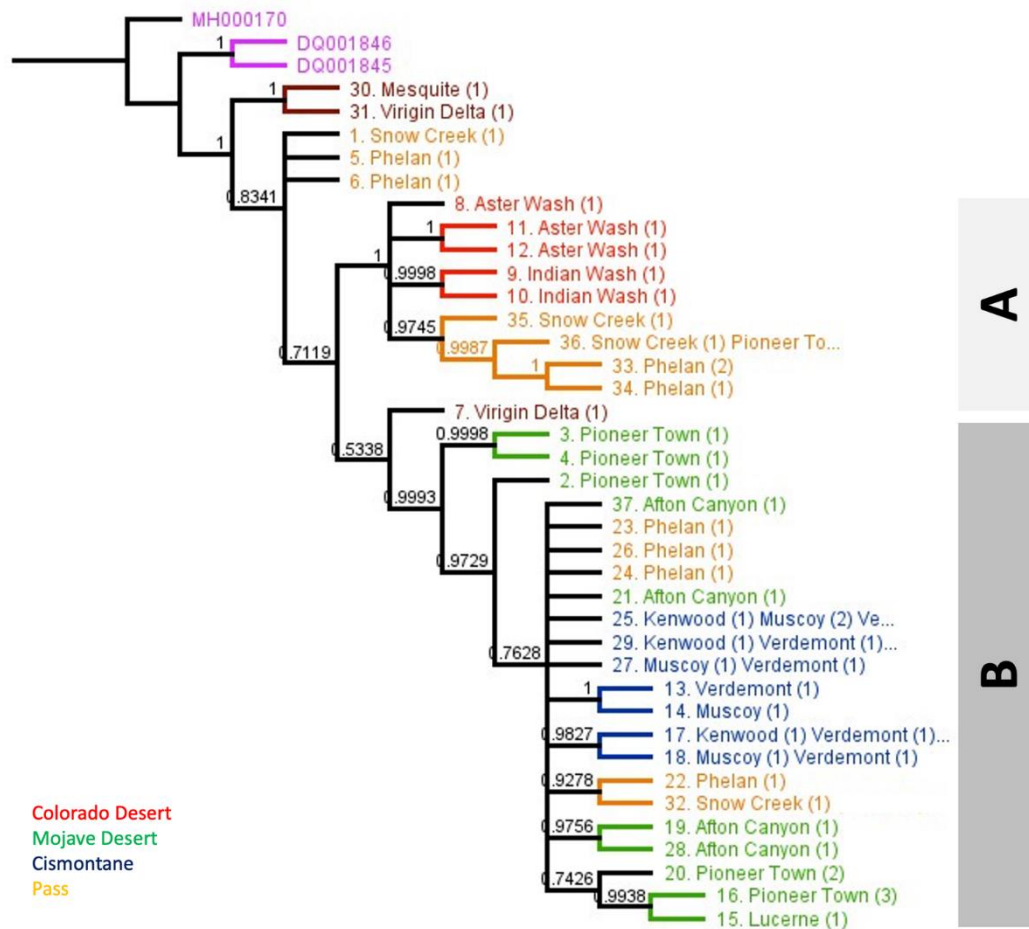


Figure 6. A Bayesian phylogenetic tree based on ATPase haplotype sequence. HKY85 genetic model used on the 37 haplotypes samples. The following were outgroups: Virgin Delta (NV), Mesquite (NV), MH000170 (Roelke and et.al, 2017), DQ001802 and DQ001803 (Lindell and et.al, 2005). MH000170 is a *Holbrookia lacerate* individual used to root the phylogenetic tree. DQ001802 is a *Callisaurus brevipes* and DQ001803 is a *Callisaurus bogerti* (Lindell et al., 2005). Clade A includes Colorado Desert, Snow Creek and Phelan individuals. Clade B has Mojave Desert, Cismontane and Pass individuals.

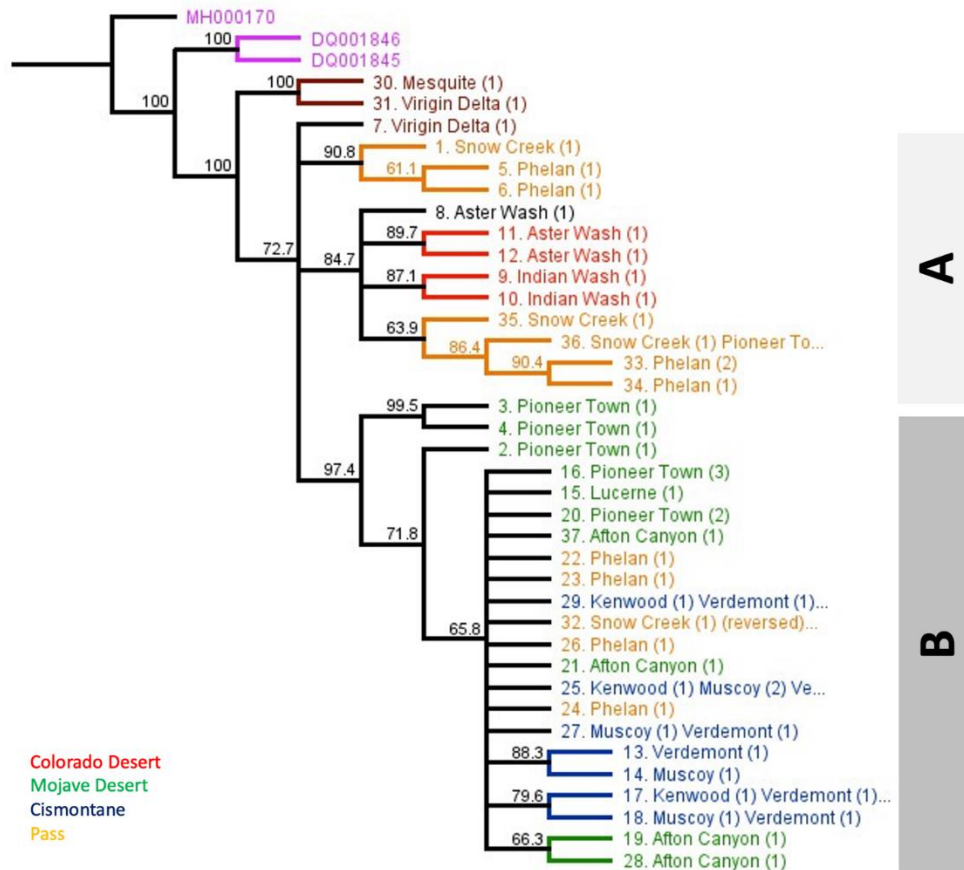


Figure 7. A Neighbor- Joining phylogenetic tree based on ATPase haplotype sequence. HKY85 genetic model used on the 37 haplotypes samples. The following were outgroups: Virgin Delta (NV), Mesquite (NV), MH000170 (Roelke and et.al, 2017), DQ001802 and DQ001803 (Lindell and et.al, 2005). MH000170 is a *Holbrookia lacerate* individual used to root the phylogenetic tree. DQ001802 is a *Callisaurus brevipes* and DQ001803 is a *Callisaurus bogerti* (Lindell et al., 2005). Clade A includes Colorado Desert, Snow Creek and Phelan individuals. Clade B has Mojave Desert, Cismontane and Pass individuals.

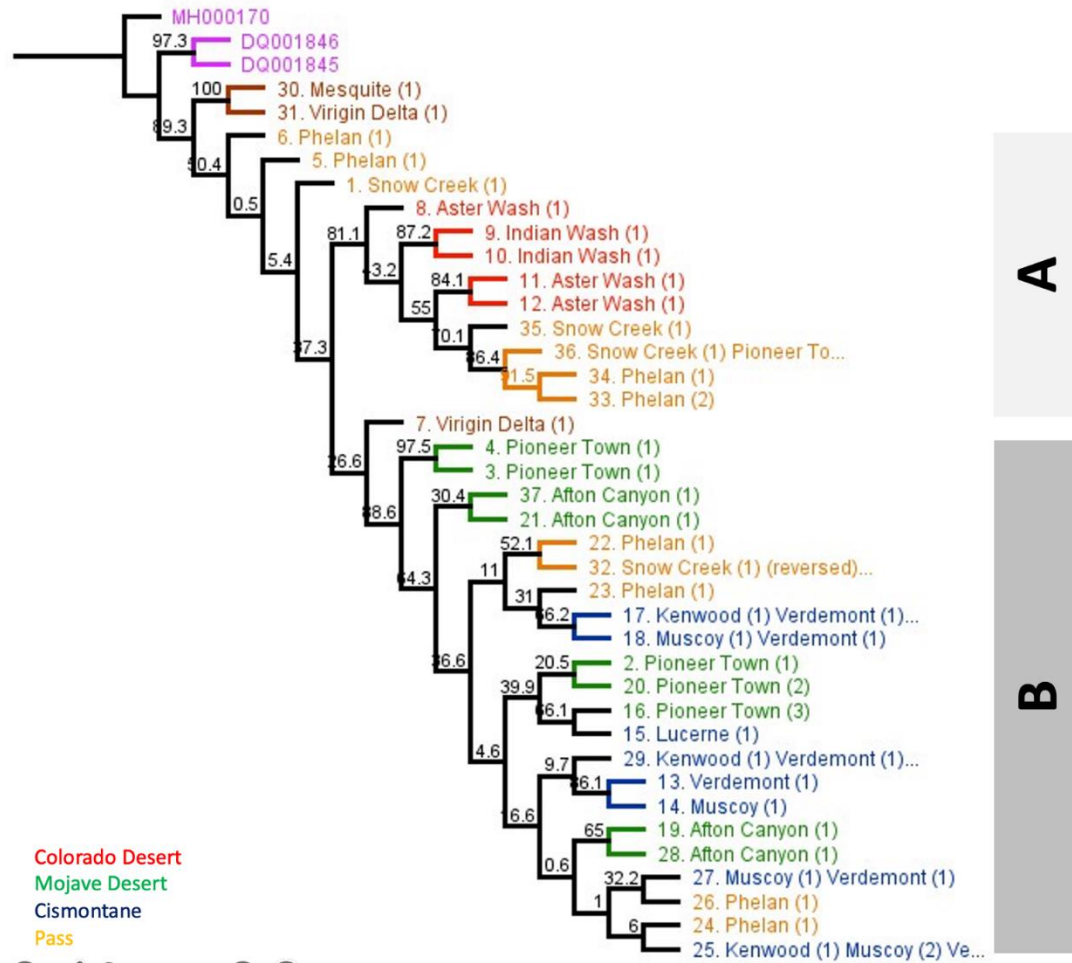


Figure 8. A Maximum Likelihood phylogenetic tree based on ATPase haplotype sequence. HKY85 genetic model used on the 37 haplotypes samples. The following were outgroups: Virgin Delta (NV), Mesquite (NV), MH000170 (Roelke and et.al, 2017), DQ001802 and DQ001803 (Lindell and et.al, 2005). MH000170 is a *Holbrookia lacerate* individual used to root the phylogenetic tree. DQ001802 is a *Callisaurus brevipes* and DQ001803 is a *Callisaurus bogerti* (Lindell et al., 2005). Clade A includes Colorado Desert, Snow Creek and Phelan individuals. Clade B has Mojave Desert, Cismontane and Pass admixture.

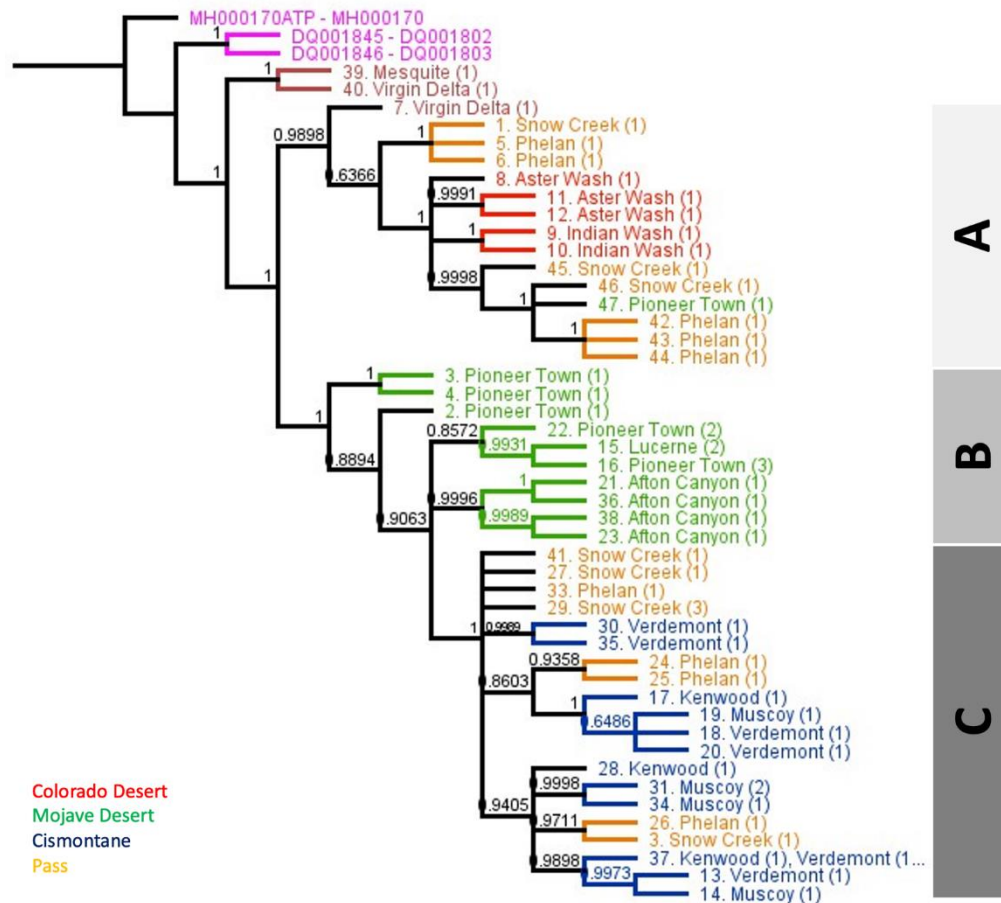


Figure 9. A Bayesian phylogenetic tree based on Concatenated mtDNA haplotype sequence. HKY85 genetic model used on the 47 haplotypes samples. The following were outgroups: Virgin Delta (NV), Mesquite (NV), MH000170 (Roelke and et.al, 2017), DQ001802 and DQ001803 (Lindell and et.al, 2005). MH000170 is a *Holbrookia lacerate* individual used to root the phylogenetic tree. DQ001802 is a *Callisaurus brevipes* and DQ001803 is a *Callisaurus bogerti* (Lindell et al., 2005). Clade A includes Colorado Desert and Phelan individuals. Clade B only has Mojave Desert individuals. Clade C has cismontane, Cajon and Banning pass individuals.

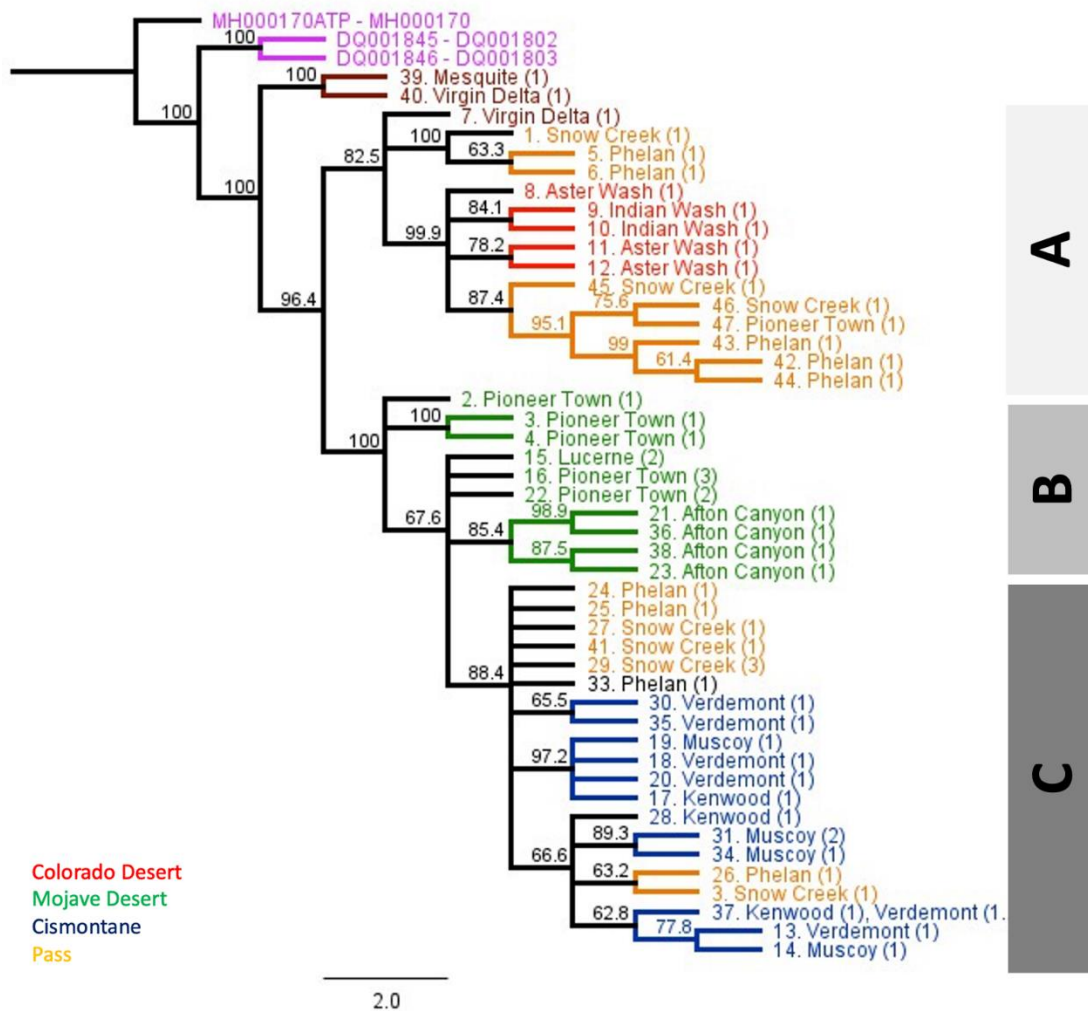


Figure 10. A Neighbor-Joining phylogenetic tree based on Concatenated mtDNA haplotype sequence. HKY85 genetic model used on the 47 haplotypes samples. The following were outgroups: Virgin Delta (NV), Mesquite (NV), MH000170 (Roelke and et.al, 2017), DQ001802 and DQ001803 (Lindell and et.al, 2005). MH000170 is a *Holbrookia lacerate* individual used to root the phylogenetic tree. DQ001802 is a *Callisaurus brevipes* and DQ001803 is a *Callisaurus bogerti* (Lindell et al., 2005). Clade A includes Colorado Desert and Phelan individuals. Clade B only has Mojave Desert individuals. Clade C has cismontane, Cajon and Banning pass individuals.

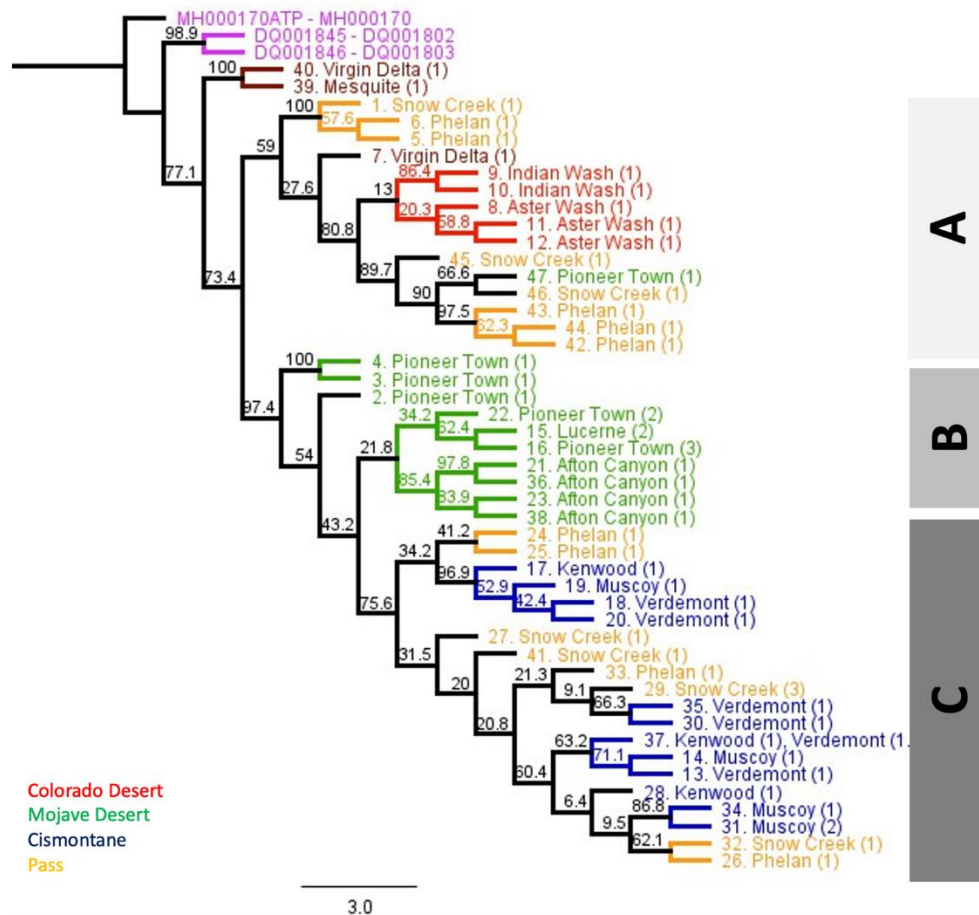


Figure 11. A Maximum Likelihood phylogenetic tree based on Concatenated mtDNA haplotype sequence. HKY85 genetic model used on the 47 haplotypes samples. The following were outgroups: Virgin Delta (NV), Mesquite (NV), MH000170 (Roelke and et.al, 2017), DQ001802 and DQ001803 (Lindell and et.al, 2005). MH000170 is a *Holbrookia lacerate* individual used to root the phylogenetic tree. DQ001802 is a *Callisaurus brevipes* and DQ001803 is a *Callisaurus bogerti* (Lindell et al., 2005). Clade A includes Colorado Desert and Phelan individuals. Clade B only has Mojave Desert individuals. Clade C has cismontane, Cajon and Banning pass individuals.

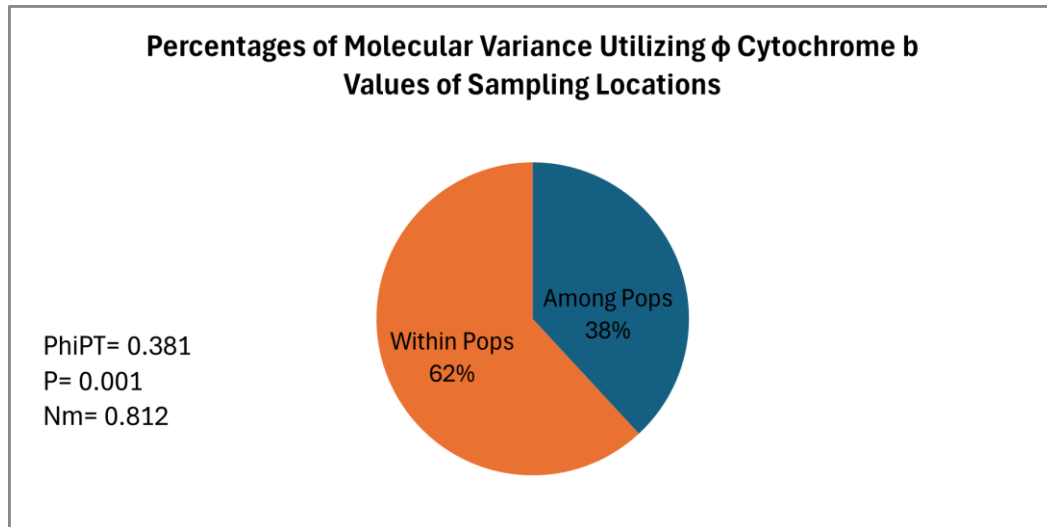


Figure 12. Percentage of molecular variance within and among the eleven sampling locations as a result from the AMOVA analysis of the cytochrome b amplicon. Include the PhiPT, P and Nm values.

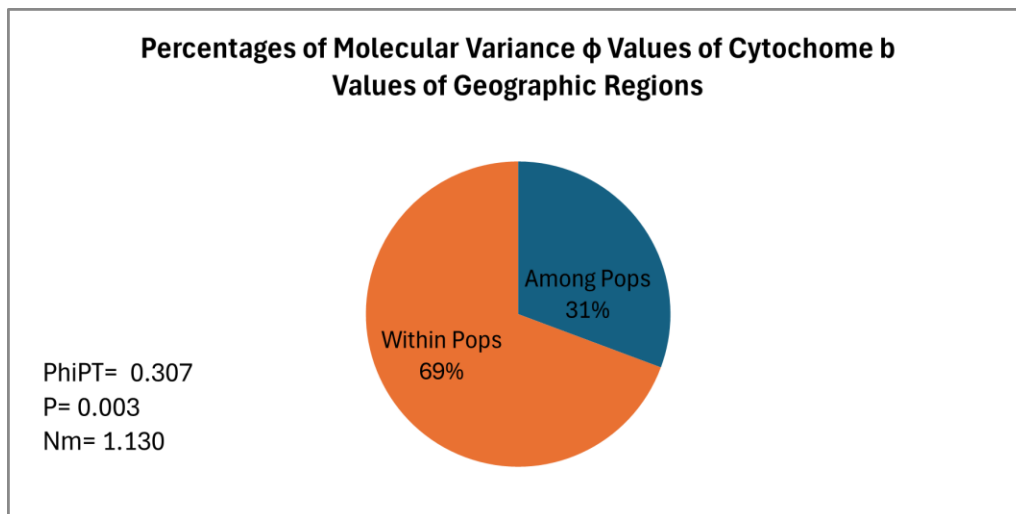


Figure 13. Percentage of molecular variance within and among the geographic region that the eleven sampling locations make up. This is a result from the AMOVA analysis of the cytochrome b amplicon. Include the PhiPT, P and Nm values.

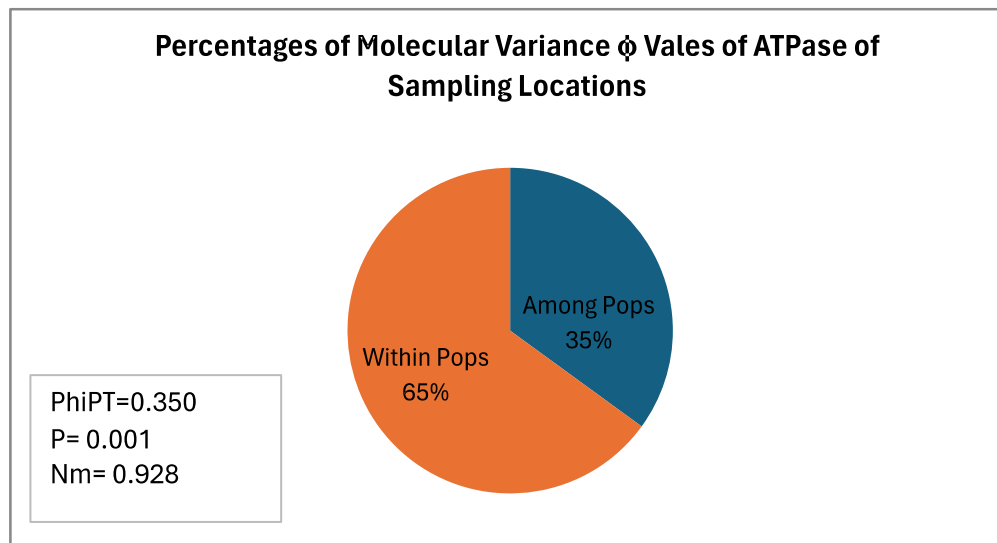


Figure 14. Percentage of molecular variance within and among the eleven sampling locations. This is a result from the AMOVA analysis of the ATPase amplicon. Include the PhiPT, P and Nm values.

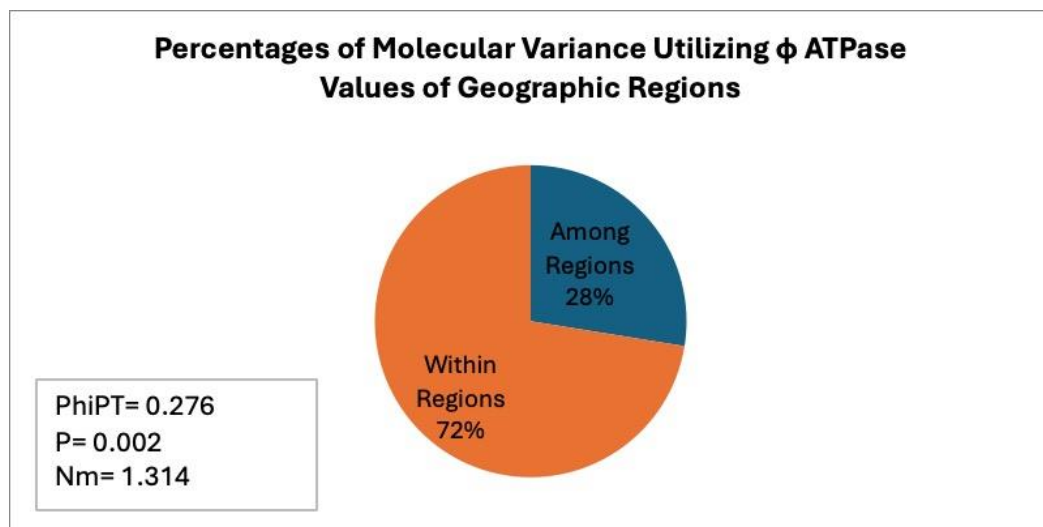


Figure 15. Percentage of molecular variance within and among the geographic region that the eleven sampling locations make up. This is a result from the AMOVA analysis of the ATPase amplicon. Include the PhiPT, P and Nm values.

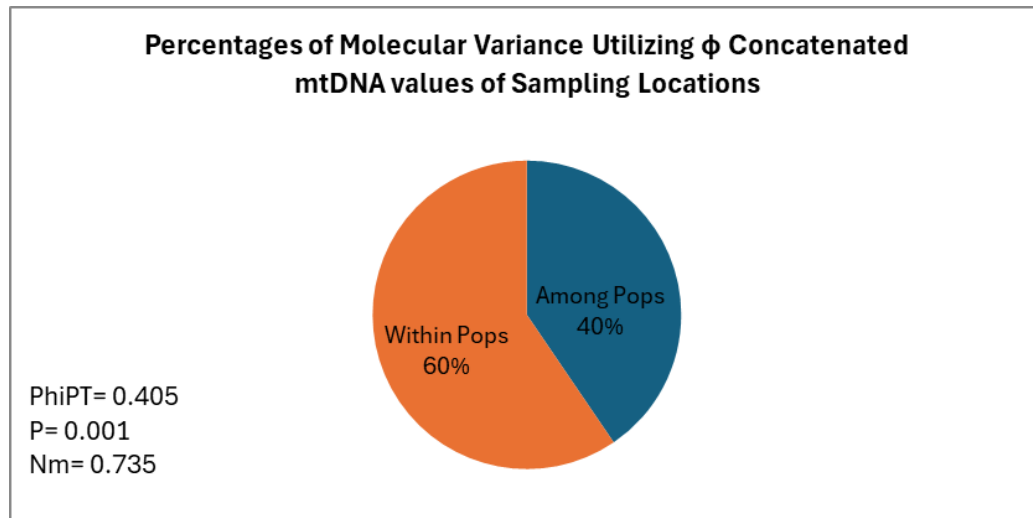


Figure 16. Percentage of molecular variance within and among the eleven sampling locations. This is a result from the AMOVA analysis of the concatenated mtDNA amplicons. Include the PhiPT, P and Nm values.

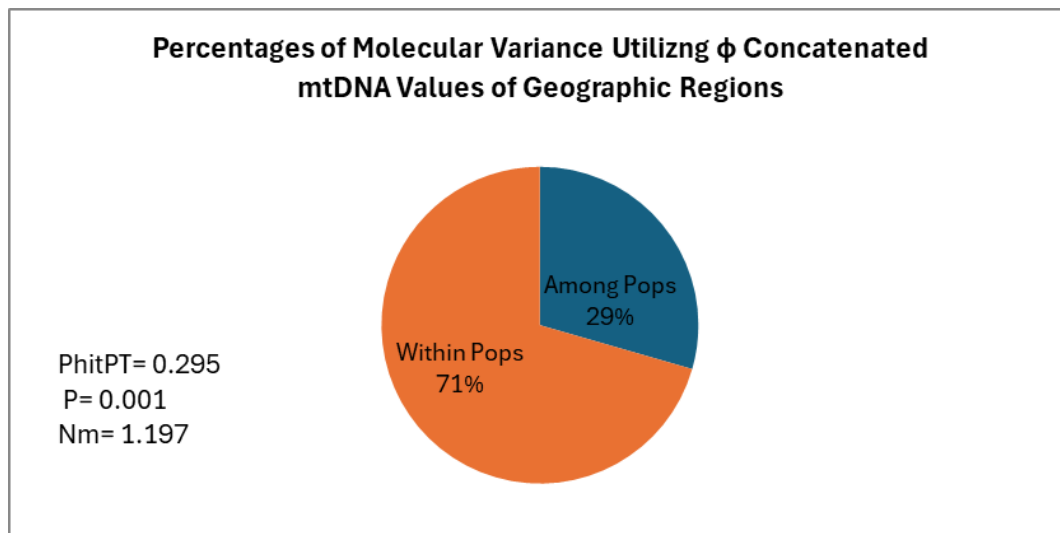


Figure 17. Percentage of molecular variance within and among the geographic region that the eleven sampling locations make up. This is a result from the AMOVA analysis of the concatenated mtDNA amplicons. Include the PhiPT, P and Nm values.

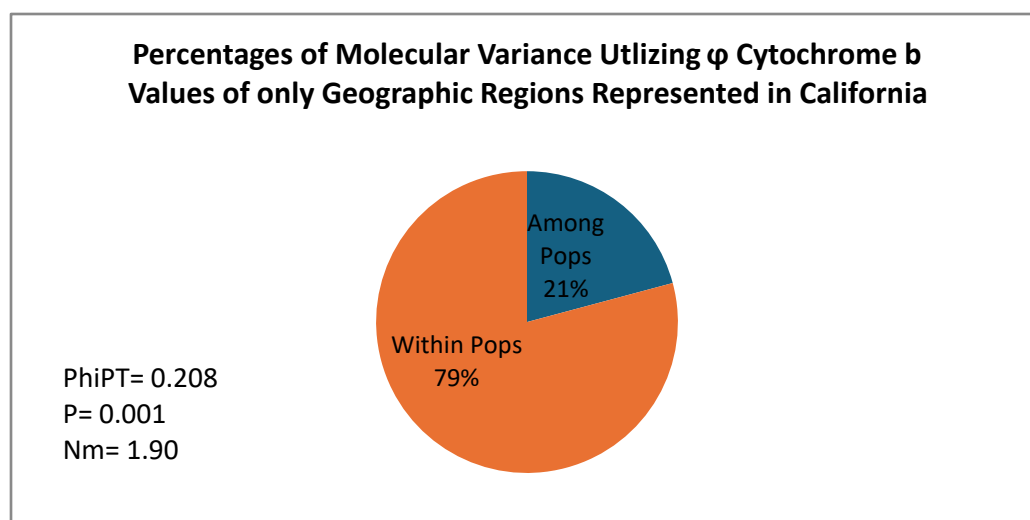


Figure 18. Percentage of molecular variance within and among the geographic region that the ten California sampling locations make up. Therefore, there are no Nevada individuals used in this analysis. This is a result from the AMOVA analysis of the cytochrome b mtDNA amplicons. Include the PhiPT, P and Nm values.

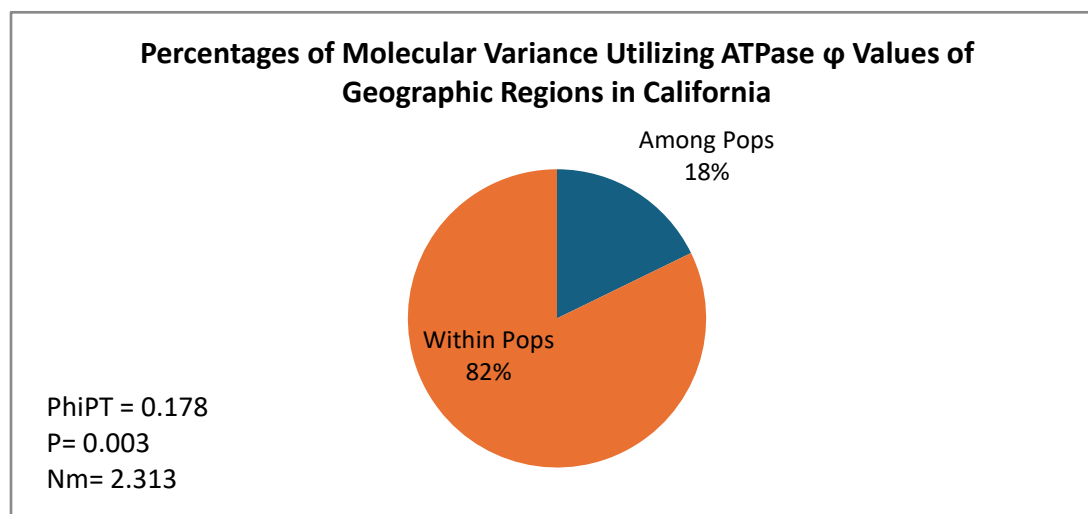


Figure 19. Percentage of molecular variance within and among the geographic region that the ten California sampling locations make up. Therefore, there are no Nevada individuals used in this analysis. This is a result from the AMOVA analysis of the ATPase mtDNA amplicons. Include the PhiPT, P and Nm values

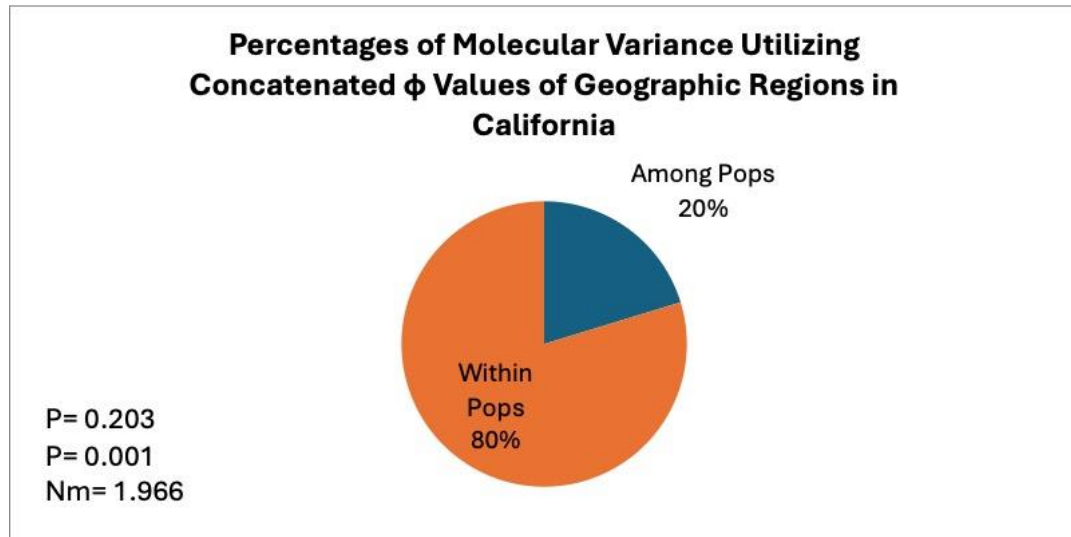


Figure 20. Percentage of molecular variance within and among the geographic region that the ten California sampling locations make up. Therefore, there are no Nevada individuals used in this analysis. This is a result from the AMOVA analysis of the Concatenated mtDNA amplicons. Include the Φ_{PT} , P and Nm values.

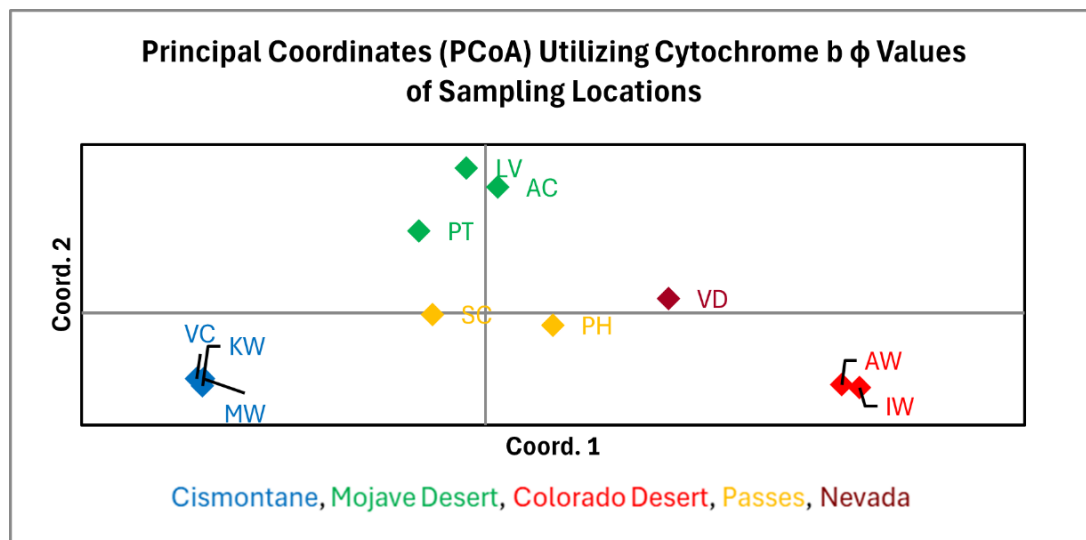


Figure 21. PCoA of the genetic dissimilarity of cytochrome b DNA sequence using the ϕ_{PT} values from the AMOVA analysis for the sampling locations.

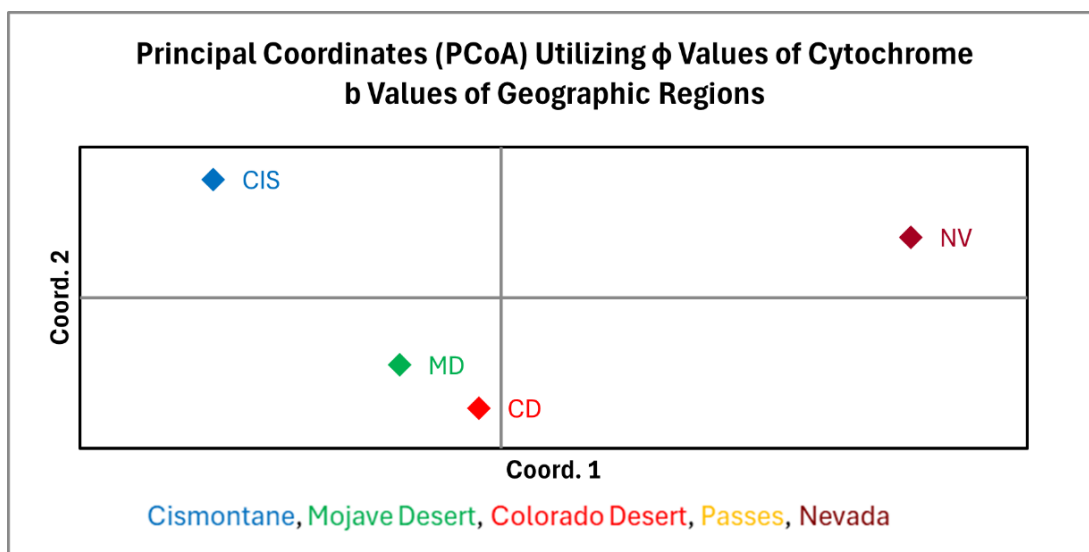


Figure 22. PCoA of the genetic dissimilarity of cytochrome b DNA sequence using the ϕ_{PT} values from the AMOVA analysis for the geographic regions.

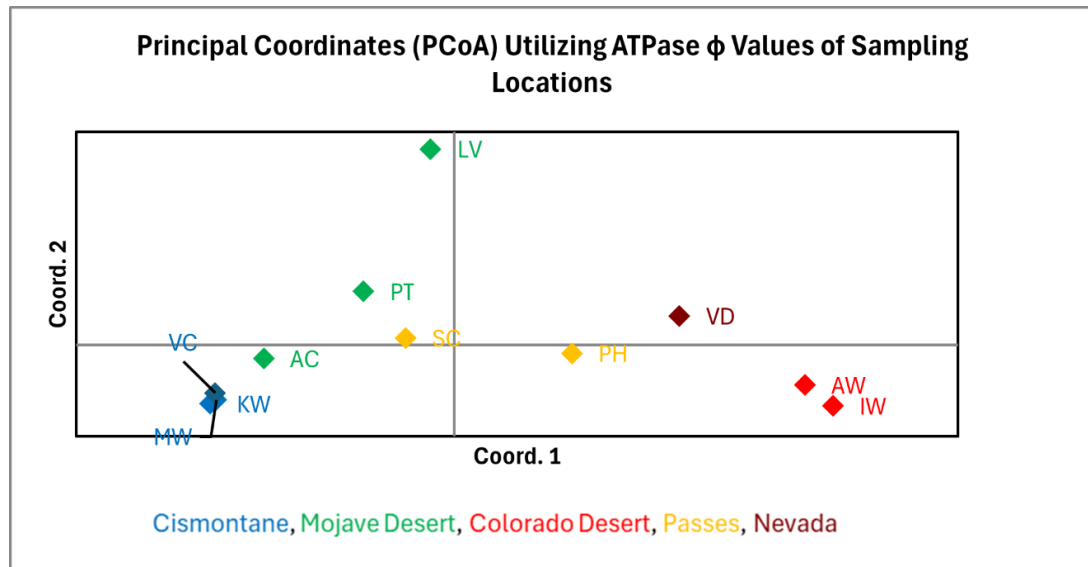


Figure 23. PCoA of the genetic dissimilarity of ATPase DNA sequence using the ϕ_{PT} values from the AMOVA analysis for the sampling locations.

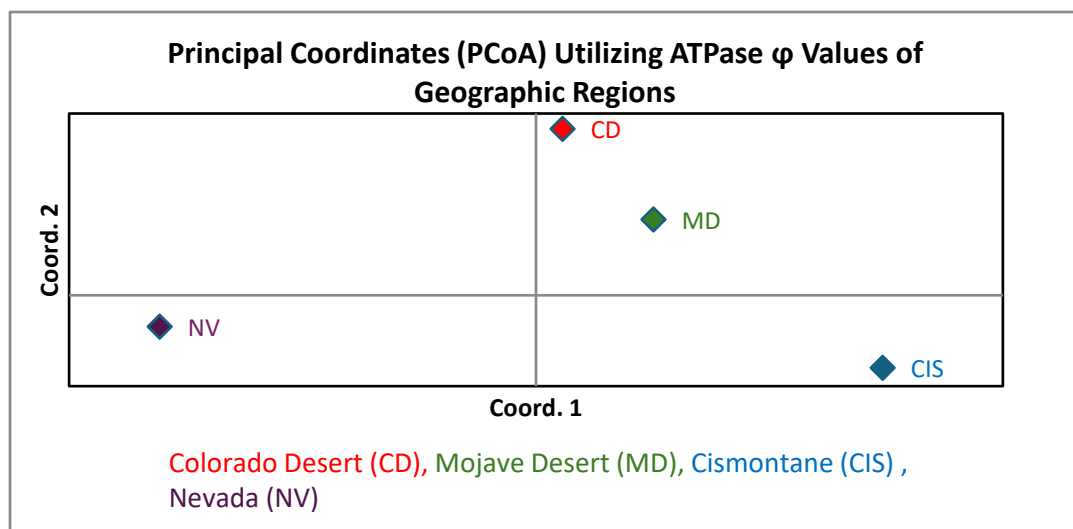


Figure 24. PCoA of the genetic dissimilarity of ATPase DNA sequence using the ϕ_{PT} values from the AMOVA analysis for the geographic regions.

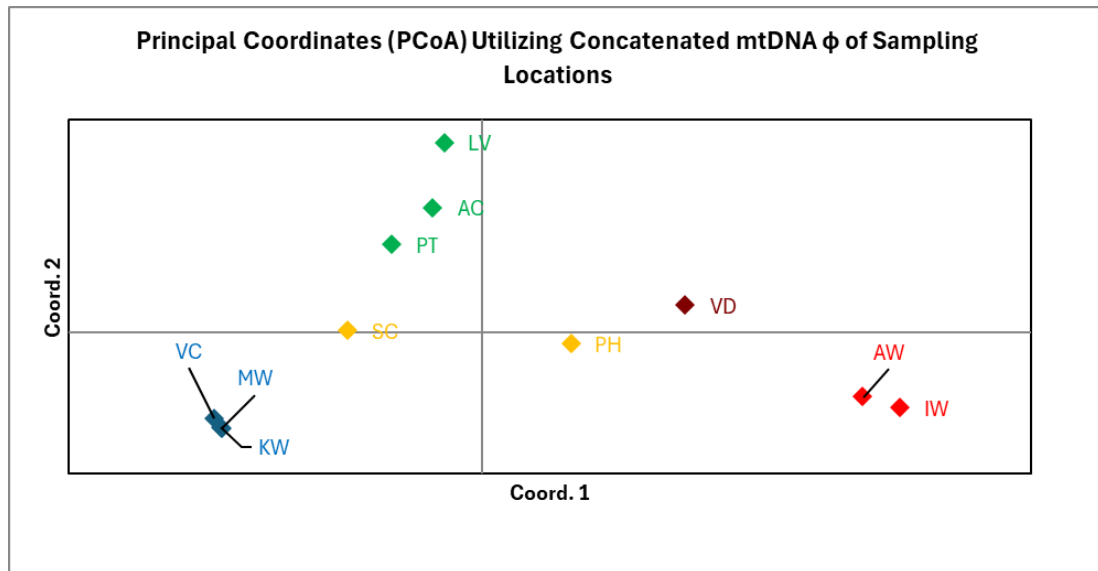


Figure 25. PCoA of the genetic dissimilarity of concatenated mtDNA sequences using the ϕ_{PT} values from the AMOVA analysis for the sampling locations.

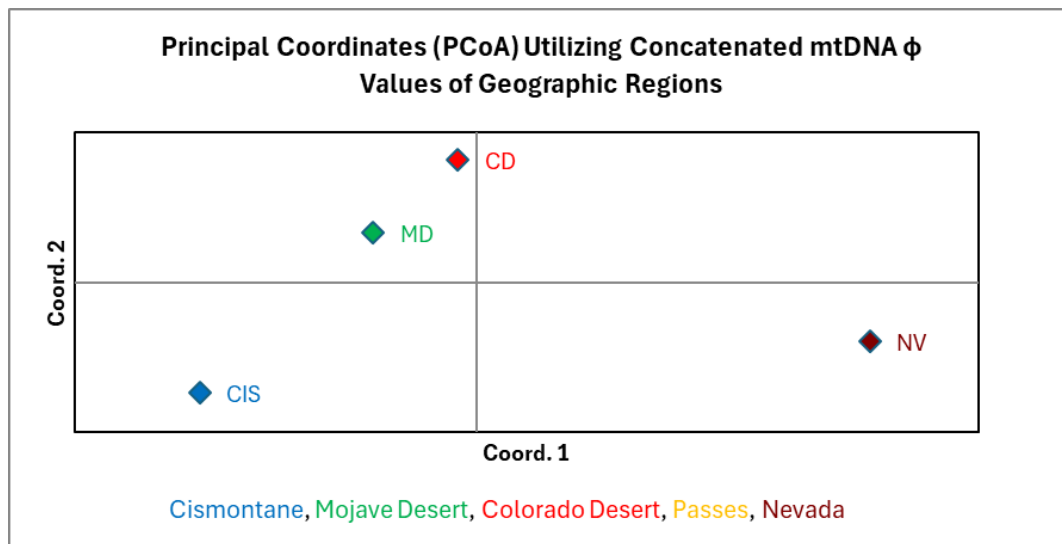


Figure 26. PCoA of the genetic dissimilarity of concatenated mtDNA sequences using the ϕ_{PT} values from the AMOVA analysis for the geographic regions.

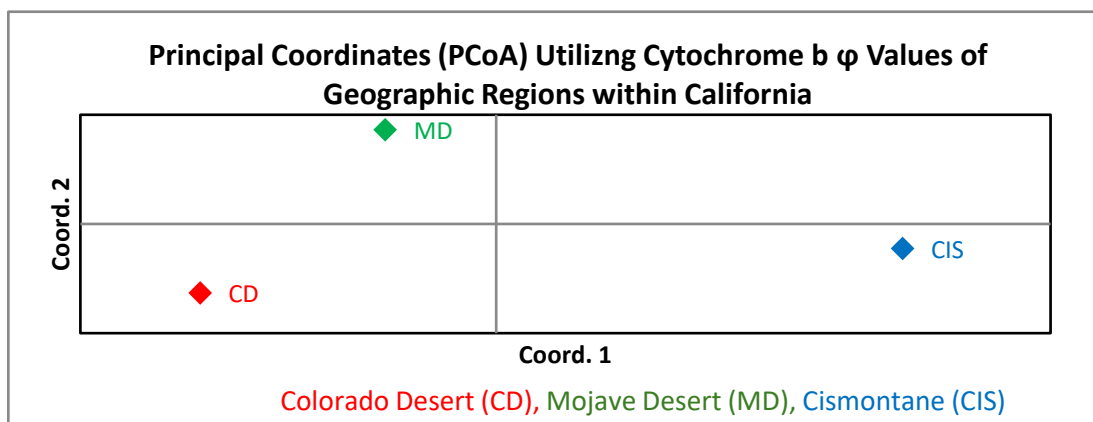


Figure 27. PCoA of the genetic dissimilarity of concatenated mtDNA sequences using the ϕ_{PT} values from the AMOVA analysis for the geographic regions.

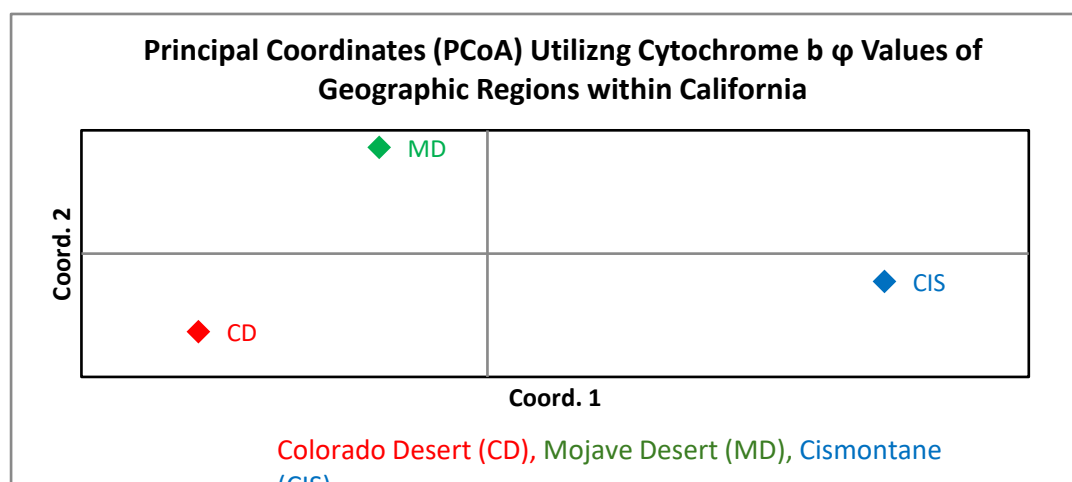


Figure 28. PCoA of the genetic dissimilarity of cytochrome mtDNA sequences using the ϕ_{PT} values from the AMOVA analysis for the geographic regions within California; therefore, no Nevada samples were used in this study.

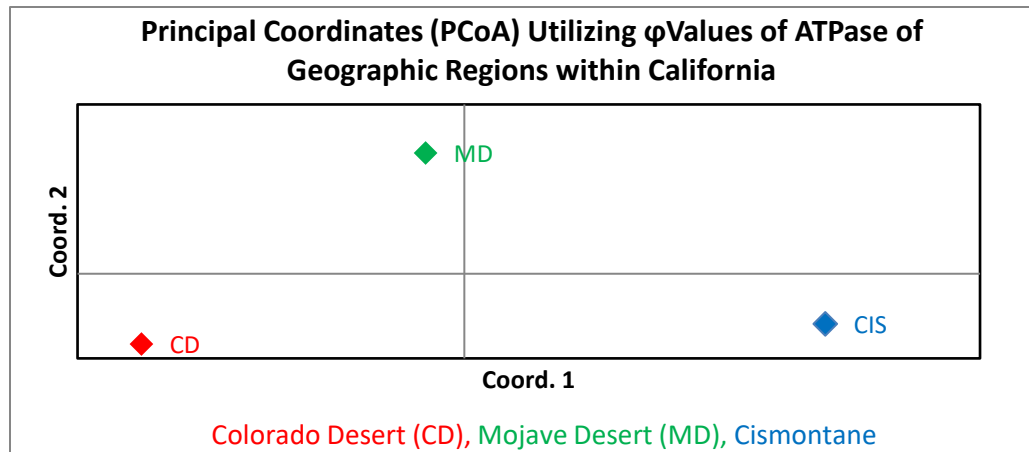


Figure 29. PCoA of the genetic dissimilarity of ATPase mtDNA sequences using the ϕ_{PT} values from the AMOVA analysis for the geographic regions within California; therefore, no Nevada samples were used in this study.

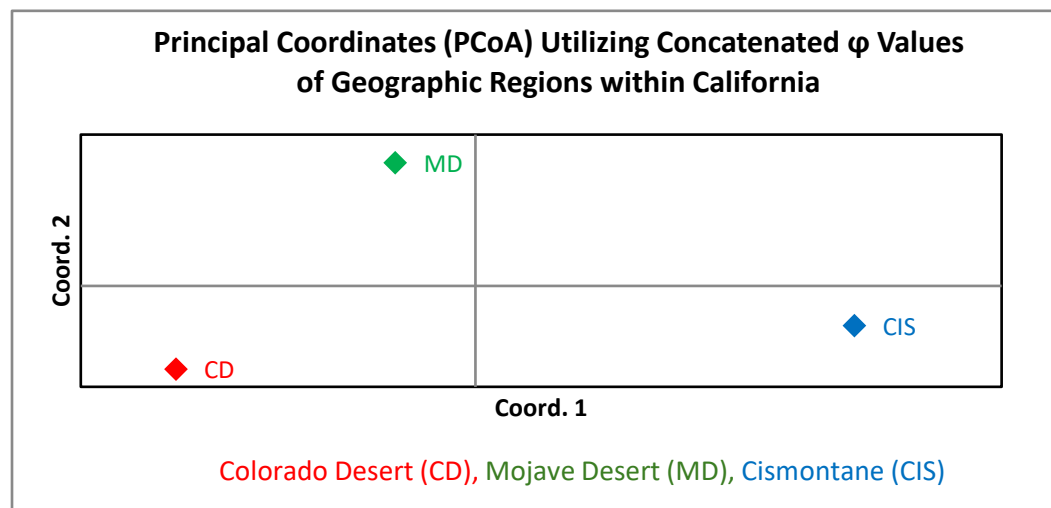


Figure 30. PCoA of the genetic dissimilarity of Concatenated mtDNA sequences using the ϕ_{PT} values from the AMOVA analysis for the geographic regions within California; therefore, no Nevada samples were used in this study.

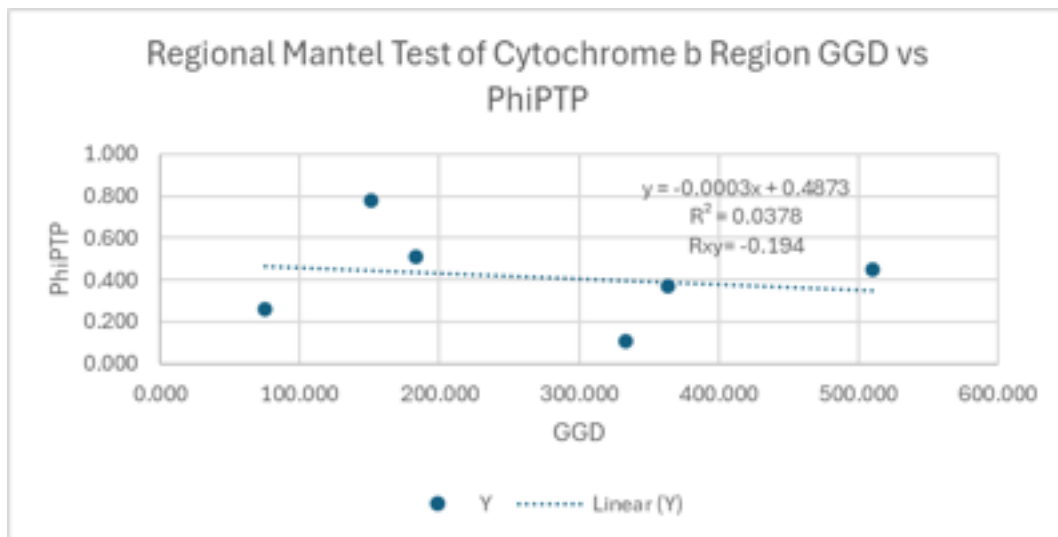


Figure 31. This is a regional mantel test done of cytochrome b PhiPT values and geographic distance.

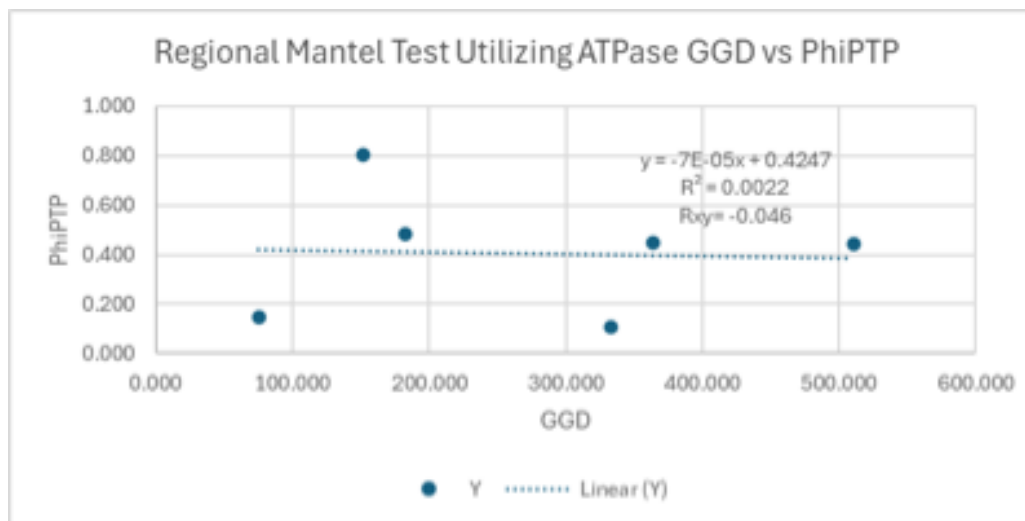


Figure 32. Above is a regional mantel done utilizing ATPase PhiPT values and geographic distance based on sampling location.

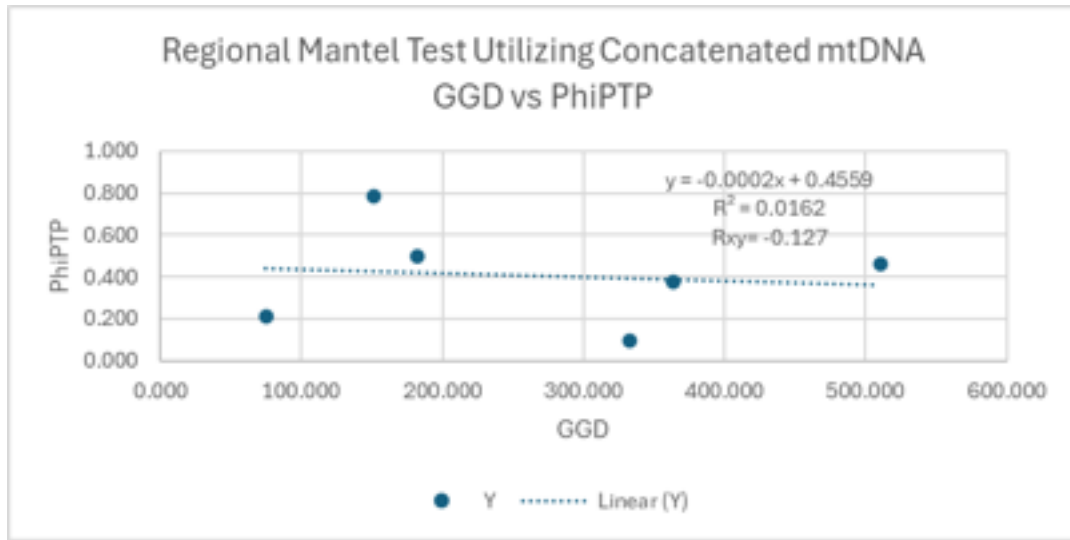


Figure 33. This figure is a regional mantel done utilizing concatenated PhiPT values and geographic distance based on sampling location.

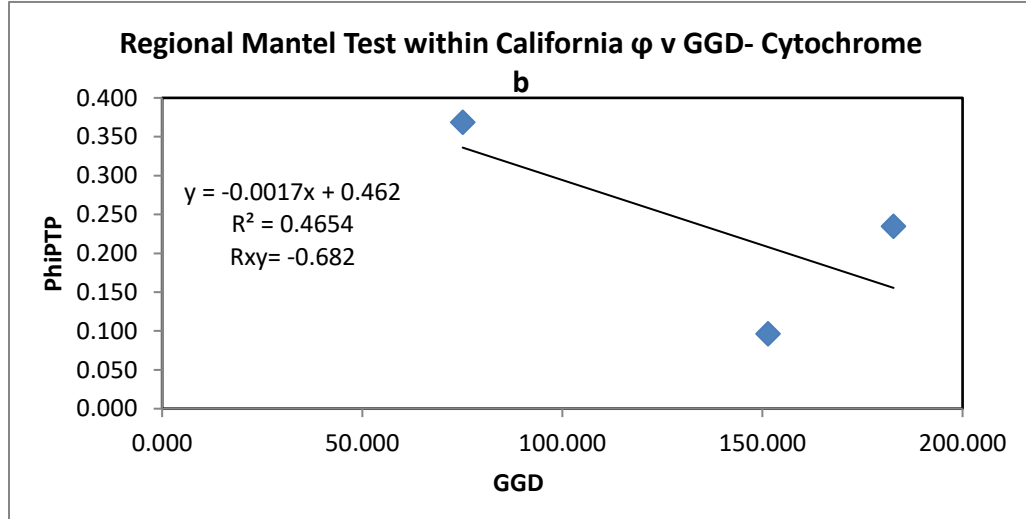


Figure 34. This figure is a regional mantel done utilizing Cytochrome b PhiPT values and geographic distance based on sampling locations within California; therefore, no Nevada samples were used in this test.

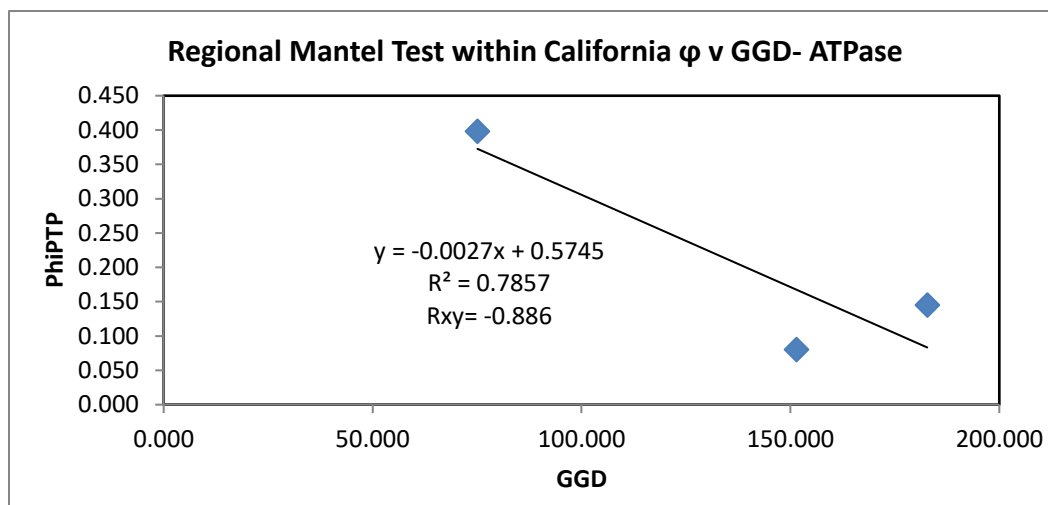


Figure 35. This figure is a regional mantel done utilizing ATPase PhiPT values and geographic distance based on sampling locations within California; therefore, no Nevada samples were used in this test.

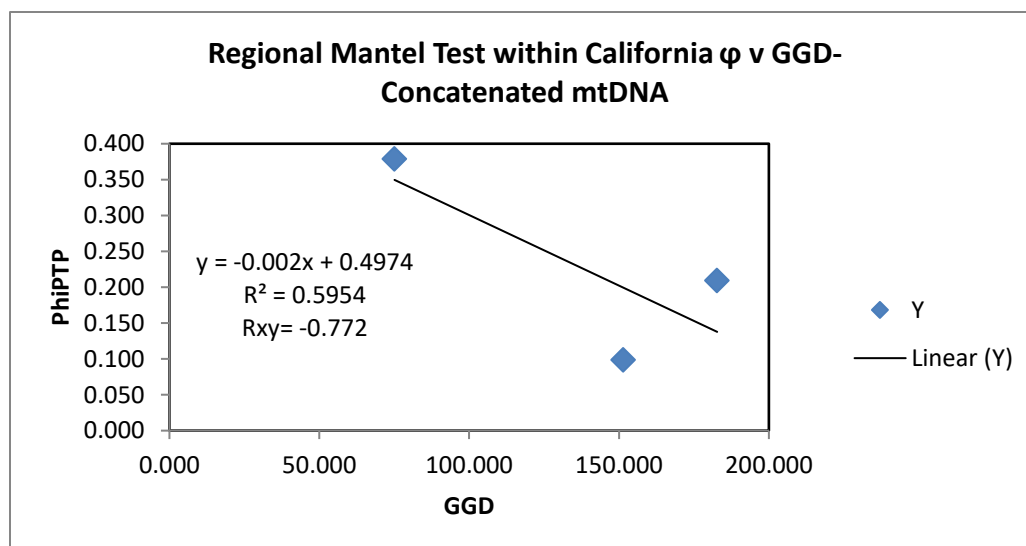


Figure 36. This figure is a regional mantel done utilizing concatenated PhiPT values and geographic distance based on sampling locations within California; therefore, no Nevada samples were used in this test.

APPENDIX B

TABLES

Table 1. Individuals amplified and sequenced. Including samples, locations, cytochrome b amplicon, San Bernardino Museum accession number.

Callisaurus Draconoides mtDNA PCR & Sequencing Progress Primer Cyt.b							
High Desert				Coastal Desert			
Location	Accession #	PCR ID	Done	Location	Accession #	PCR ID	Done
Afton Canyon	3533	AC33	X	Kenwood	3508	KW08	X
	3534	AC34	X		3509	KW09	X
	3535	AC35	X		3510	KW10	X
	3536	AC36	X	Verdemon	3569	VC69	X
Phelan Hills	3504	PH04	X		3570	VC70	X
	3505	PH05	X		3571	VC71	X
	3506	PH06	X		3572	VC72	X
	3507	PH07	X		3573	VC73	X
	3512	PH12	X		Muscoy	3511	MW11
	3513	PH13	X	3574		MW74	X
	3514	PH14	X	3575		MW75	X
	3515	PH15	X	3576		MW76	X
	3516	PH16	X	3577		MW77	X
Lucerne Valley	3537	LV37	X	3578		MW78	X
	3538	LV38	X	Nevada Samples			
Pioneer Town	3524	PT24	X	Location	Accession #	PCR ID	Done
	3525	PT25	X	Mesquite	3586	MS86	X
	3526	PT26	X	Virgin Delta	3584	VD84	X
	3527	PT27	X		3585	VD85	X
	3528	PT28	X				
	3529	PT29	X				
	3530	PT30	X				
	3531	PT31	X				
	3532	PT32	X				
Jawbone	3581	JC81	X				
Low Desert							
Location	Accession #	PCR ID	Done				
Snow Creek	3500	SC00	X				
	3501	SC01	X				
	3502	SC02	X				
	3503	SC03	X				
	3504	SC04	X				
	3518	SC18	X				
	3519	SC19	X				
	3520	SC20	X				
	3521	SC21	X				
	3522	SC22	X				
	3523	SC23	X				
Aster Wash	3540	AW40	X				
	3541	AW41	X				
	3542	AW42	X				
Indian Wash	3582	IW82	X				
	3583	IW83	X				

Table 2. Individuals amplified and sequenced. Including samples, locations, ATPase amplicon, San Bernardino Museum accession number.

Callisaurus Draconoides mtDNA PCR & Sequencing Progress Primer ATPase							
High Desert				Coastal Desert			
Location	Accession #	PCR ID	Done	Location	Accession #	PCR ID	Done
Afton Canyon	3533	AC33	X	Kenwood	3508	KW08	X
	3534	AC34	X		3509	KW09	X
	3535	AC35	X		3510	KW10	X
	3536	AC36	X	Verdemont	3569	VC69	X
Phelan Hills	3504	PH04	X		3570	VC70	X
	3505	PH05	X		3571	VC71	X
	3506	PH06	X		3572	VC72	X
	3507	PH07	X		3573	VC73	X
	3512	PH12	X	Muscoy	3511	MW11	X
	3513	PH13	X		3574	MW74	X
	3514	PH14	X		3575	MW75	
	3515	PH15	X		3576	MW76	X
	3516	PH16	X		3577	MW77	X
Lucerne Valley	3537	LV37	X		3578	MW78	X
	3538	LV38	X	Nevada Samples			
Pioneer Town	3524	PT24	X	Location	Accession #	PCR ID	Done
	3525	PT25	X	Mesquite	3586	MS86	X
	3526	PT26	X	Virgin Delta	3584	VD84	X
	3527	PT27	X		3585	VD85	X
	3528	PT28	X				
	3529	PT29	X				
	3530	PT30	X				
	3531	PT31	X				
	3532	PT32	X				
Jawbone	3581	JC81					
Low Desert							
Location	Accession #	PCR ID	Done				
Snow Creek	3500	SC00	X				
	3501	SC01	X				
	3502	SC02	X				
	3503	SC03					
	3504	SC04	X				
	3518	SC18	X				
	3519	SC19	X				
	3520	SC20	X				
	3521	SC21	X				
	3522	SC22	X				
	3523	SC23	X				
	3540	AW40	X				
Aster Wash	3541	AW41	X				
	3542	AW42	X				
Indian Wash	3582	IW82	X				
	3583	IW83	X				

Table 3. Individuals amplified and sequenced. Including samples, locations, concatenated mtDNA amplicons, San Bernardino Museum accession number.

Callisaurus Draconoides mtDNA PCR & Sequencing Progress Primer AT3							
High Desert				Coastal Desert			
Location	Accession #	PCR ID	Done	Location	Accession #	PCR ID	Done
Afton Canyon	3533	AC33	X	Kenwood	3508	KW08	X
	3534	AC34	X		3509	KW09	X
	3535	AC35	X		3510	KW10	X
	3536	AC36			3569	VC69	
Phelan Hills	3504	PH04	X	Verdemont	3570	VC70	
	3505	PH05			3571	VC71	
	3506	PH06	X		3572	VC72	
	3507	PH07	X		3573	VC73	X
	3512	PH12	X	Muscoy	3511	MW11	X
	3513	PH13	X		3574	MW74	
	3514	PH14	X		3575	MW75	
	3515	PH15	X		3576	MW76	X
	3516	PH16	X		3577	MW77	
	3537	LV37	X		3578	MW78	X
Lucerne Valley	3538	LV38		Nevada Samples			
Pioneer Town	3524	PT24		Location	Accession #	PCR ID	Done
	3525	PT25	X	Mesquite	3586	MS86	X
	3526	PT26		Virgin Delta	3584	VD84	
	3527	PT27	X		3585	VD85	
	3528	PT28	X				
	3529	PT29	X				
	3530	PT30					
	3531	PT31	X				
	3532	PT32	X				
Jawbone	3581	JC81	X				
Low Desert							
Location	Accession #	PCR ID	Done				
Snow Creek	3500	SC00					
	3501	SC01					
	3502	SC02	X				
	3503	SC03	X				
	3504	SC04					
	3518	SC18	X				
	3519	SC19	X				
	3520	SC20	X				
	3521	SC21	X				
	3522	SC22	X				
	3523	SC23	X				
	3540	AW40	X				
Aster Wash	3541	AW41					
	3542	AW42	X				
Indian Wash	3582	IW82	X				
	3583	IW83	X				

Table 4. Cytochrome b haplotype list including haplotype code, number of individuals per haplotype, geographic and sampling location represented in that haplotype.

Cytochrome b Haplotype List			
Haplotype Code	Count	Geographic Region	Sampling location
1	1	Low Desert	AW
2	1	Low Desert	AW
3	1	High Desert Pass	PH
4	2	High Desert Pass	PH,PH
5	1	Low Desert	AW
6	1	Low Desert	IW
7	1	Low Desert	IW
8	1	Low Desert Pass	SC
9	1	Low Desert Pass	SC
10	1	High Desert	PT
11	1	High Desert	AC
12	1	High Desert	AC
13	4	Low and High Desert Pass	PH, PH, SC,SC
14	1	Cismontane	MW
15	1	Nevada	VD
16	1	Nevada	VD
17	1	Low Desert Pass	SC
18	1	Low Desert Pass	SC
19	2	Cismontane	KW, VC
20	3	Cismontane	VC, MW, KW
21	4	Low and High Desert Pass	PH,SC,SC,SC
22	2	Cismontane	VC, VC
23	1	High Desert Pass	PH
24	1	High Desert Pass	PH
25	1	High Desert	AC
26	2	High Desert	PT,PT
27	2	High Desert	LV, LV
28	3	High Desert	PT,PT,PT
29	2	High Desert	PT, PT
30	1	High Desert	AC
31	1	High Desert	PT
32	2	Cismontane	MW,MW
33	1	Cismontane	MW
34	2	Cismontane	MW, KW
35	2	Cismontane	VC, VC
36	2	Low and High Desert Pass	SC, PH

Table 5. ATPase Haplotype code, number of individuals per haplotype, geographic and sampling location represented in that haplotype.

ATPase Haplotype List			
Haplotype Code	Count	Geographic Region	Sampling Location
1	1	Low Desert Pass	SC
2	1	High Desert	PT
3	1	High Desert	PT
4	1	High Desert	PT
5	1	High Desert Pass	PH
6	1	High Desert Pass	PH
7	1	Nevada	VD
8	1	Low Desert	AW
9	1	Low Desert	IW
10	1	Low Desert	IW
11	1	Low Desert	AW
12	1	Low Desert	AW
13	1	Cismontane	CIS
14	1	Cismontane	CIS
15	1	High Desert	LV
16	3	High Desert	PT
17	2	Cismontane	KW (1), VC (1)
18	2	Cismontane	MW,VC
19	1	High Desert	AC
20	2	High Desert	PT (2)
21	1	High Desert	AC
22	1	High Desert Pass	PH
23	1	High Desert Pass	PH
24	1	High Desert Pass	PH
25	9	Cismontane and Low Desert Pass	KW (1),VC (1), MW (2), SC (5)
26	1	High Desert Pass	PH
27	2	Cismontane	MW (1),VC (1)
28	1	High Desert	AC
29	2	Cismontane	KW (1), VC(1)
30	1	Nevada	MS
31	1	Nevada	VD
32	1	Low Desert Pass	SC
33	2	High Desert Pass	PH (2)
34	1	High Desert Pass	PH
35	1	Low Desert Pass	SC
36	2	Low Desert and High Desert Pass	SC (1),PT (1)
37	1	High Desert	AC

Table 6. Concatenated haplotype code, number of individuals per haplotype, geographic and sampling location represented in that haplotype.

Concatenated Haplotype List			
Haplotype Code	Count	Geographic Region	Sampling Location
1	1	Low Desert Pass	SC
2	1	High Desert	PT
3	1	High Desert	PT
4	1	High Desert	PT
5	1	High Desert Pass	PH
6	1	High Desert Pass	PH
7	1	Nevada	VD
8	1	Low Desert	AW
9	1	Low Desert	IW
10	1	Low Desert	IW
11	1	Low Desert	AW
12	1	Low Desert	AW
13	1	Cismontane	VC
14	1	Cismontane	MW
15	2	High Desert	LV (2)
16	3	High Desert	PT (3)
17	1	Cismontane	KW
18	1	Cismontane	VC
19	1	Cismontane	MW
20	1	Cismontane	VC
21	1	High Desert	AC
22	2	High Desert	PT (2)
23	1	High Desert	AC
24	1	High Desert Pass	PH
25	1	High Desert Pass	PH
26	1	High Desert Pass	PH
27	1	Low Desert Pass	SC
28	1	Cismontane	KW
29	3	Low Desert Pass	SC
30	1	Cismontane	VC
31	2	Cismontane	MW (2)
32	1	Low Desert Pass	SC
33	1	High Desert Pass	PH
34	1	Cismontane	MW
35	1	Cismontane	VC
36	1	High Desert	AC
37	2	Cismontane	KW(1), VC(1)
38	1	High Desert	AC
39	1	Nevada	MS
40	1	Nevada	VD
41	1	Low Desert Pass	SC
42	1	High Desert Pass	PH
43	1	High Desert Pass	PH
44	1	High Desert Pass	PH
45	1	Low Desert Pass	SC
46	1	Low Desert Pass	SC
47	1	High Desert	PT

Table 7. Polymerase chain reaction (PCR) reaction mixture formula.

Polymerase Chain Reaction Mixture	
DNA	1ul
Forward (or Heavy)Primer	1ul
Reverse (or Light) Primer	1ul
Purified Water	22ul
Taq DNA polymerase	0.5U/ul
MgCl ₂	4mM
dNTP	0.4 mM

Table 8. Cytochrome b (mtDNA), ATPase (mtDNA) and Alpha-Tubulin (nuclear DNA) PCR protocols

Adenosine Triphosphatase-6 (866)		
Initial Denaturation	94°C	5 minutes
35 cycles		
Denature	94°C	1 minute
Annealing	50.7	30 seconds
Elongate	72°C	1 minute
Final Extension	72°C	1 minute
Alpha-Tubulin (650bp)		
Initial Denaturation	94°C	5 minutes
35 cycles		
Denature	94°C	1 minute
Annealing	50.7	30 seconds
Elongate	72°C	1 minute
Final Extension	72°C	1 minute
Cytochrome b (1044 bp)		
Initial Denaturation	94°C	5 minutes
40 cycles		
Denature	94°C	30 seconds
Annealing	62°C	1 minute
Elongate	72°C	2 minutes
Final Extension	72°C	10 minutes

Table 8. Cytochrome b (mtDNA), ATPase (mtDNA) and Alpha-Tubulin (nuclear DNA) PCR protocols

<u>PCR Primers</u>		
<u>1. Mitochondrial Markers:</u>		Referances:
<u>Cytochrome b</u>		
L16355	5'- CCA TCC AAC ATC GCA TGA AA-3'	Lindell et al. 2005
H17415	5'-GTC TTC AGT TTT TGG TTT ACA AGA-3'	Lindell et al. 2005
<u>ATPase</u>		
L9839	5'- AGC ACT AGC CTT TTA AGY T-3'	Lindell et al. 2005
H10710	5'- GTG TGC TTG GTG TGY CAT-3'	Lindell et al. 2005
<u>2. Nuclear Markers:</u>		
<u>Alpha Tubulin</u>		
Intron 3 Forward	5'-CCC GAG CAA CTC ATC AC-3'	Blaine, 2006
Intron 4 Reverse	5'-AAC TCA AGC TTG GAC TTC TT-3'	Blaine, 2006

Table 9. Published species, gene names, accession number and length (bp) of outgroups used in study.

Outgroup Mitchrondiral Information					
Lizard Species	Collection locality	Cytochrome b Accession Number	Cytochrome B Length (bp)	ATPase Accession Number	ATPase Length (bp)
Holbrookia maculata	Mexico; Chihuahua	MH000170	1,139	MH000170ATP	850
Callisaurus brevipes	Mexico; Sonora	DQ001803	1,081	DQ001846	866
Callisaurus insitatus	Mexico; Alamos	DQ001802	1,081	DQ001845	866

Table 10. Summary of the nucleotide statistics.

Nucleotide Statistics		Cytochrome b	ATPase	Concatenated Sequences	ALPHA-TUBULIN (AT3)
Mitochondrial Gene Number		1	2	3	1
Final Aligned Length		1,140	820	1,960	538
Number of Sequences		58	55	55	35
Identical Sites		1,013 (88.9%)	750 (91.5%)	1,402 (71.5%)	534 (99.3%)
Pairwise Identity		98.40%	98.60%	97.00%	99.80%
Base Frequency	A	21,207 (32.1%)	293 (35%)	658 (33.6%)	6,154 (32.7%)
	C	17,305 (26.2%)	202 (24.6%)	501 (25%)	3,554 (18.9%)
	G	7,959 (12.0%)	85 (10.4%)	222 (11.3%)	3,612 (19.2%)
	T	19,649 (29.7%)	240 (29.3%)	579 (29.5%)	5,508 (29.3%)
GC CONTENT		25,264 (38.2%)	723 (35%)	723 (36.9%)	7,166 (38.1%)

Table 10. Transition/Transversion data derived from the concatenated sequences of mtDNA markers using HKY+G model of substitution

From\To	A	T	C	G
A	-	0.018938581	0.016427573	0.09807996
T	0.021649772	-	0.222841909	0.007230308
C	0.021649772	0.256904021	-	0.007230308
G	0.293681641	0.018938581	0.016427573	-
	Transition (Ti)	0.871507531		
	Transversion (Tv)	0.128492469		
	Ti/Tv	6.78255726		

APPENDIX C
SEQUENCE DATA

The following are Variable sites for the Concatenated mtDNA bases 1-1156

[illegible]

The following are Variable sites for the Concatenated mtDNA haplotype bases 1157-1812

[illegible]

The following are Variable sites for the Concatenated mtDNA bases 1813-1960

	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
	7	7	8	8	8	8	8	8	8	8	8	9	9	9	9	9	9	9	9
	7	8	1	1	1	2	3	4	6	7	7	8	9	0	0	1	1	2	3
	7	8	3	6	9	2	7	6	4	0	9	0	0	0	6	2	8	3	3
Consensus Sequence	A	C	T	C	C	T	A	T	C	T	T	G	C	T	A	C	C	G	C
39. Mesquite (1)				C	A	T				T	C			T		T		G	
40. Virgin Delta (1)				C	A	T				T	C			T		T		G	
3. Pioneer Town (1)			T						C									G	
4. Pioneer Town (1)			T						C									G	
2. Pioneer Town (1)																			
19. Muscoy (1)												C						G	
17. Kenwood (1)	G											C						G	
18. Verdemont (1)	G											C						G	
20. Verdemont (1)	G											C						G	
41. Snow Creek (1)																		G	
24. Phelan (1)																		G	
25. Phelan (1)																		G	
37. Kenwood (1) Verdemont (1)																			
13. Verdemont (1)																			
14. Muscoy (1)																			
31. Muscoy (2)																			
34. Muscoy (1)																			
27. Snow Creek (1)																		G	
28. Kenwood (1)																			
26. Phelan (1)																			
32. Snow Creek (1)																			
33. Phelan (1)																		G	
29. Snow Creek (3)																		G	
30. Verdemont (1)												T						G	
35. Verdemont (1)												T						G	
22. Pioneer Town (2)																		G	
15. Lucerne (2)															C			G	
16. Pioneer Town (3)																		G	
21. Afton Canyon (1)															C			G	
36. Afton Canyon (1)															C			G	
38. Afton Canyon (1)															C			G	T
23. Afton Canyon (1)															C			G	
8. Aster Wash (1)	G			C				G		T						C		A	
45. Snow Creek (1)				C						T			T			C		A	
42. Phelan (1)				C				G		T						C		A	A
43. Phelan (1)				C				G		T						C		A	A
44. Phelan (1)				C				G		T						C		A	A
46. Snow Creek (1)				C				G		T			T			C		A	A
47. Pioneer Town (1)				C				G		T			T			C		A	A
11. Aster Wash (1)				C				G		T						C		A	
12. Aster Wash (1)				C				G		T						C		A	
9. Indian Wash (1)				C				G		T						C		A	
10. Indian Wash (1)				C				G		T						C		A	T
7. Virgin Delta (1)				C				G		T									
1. Snow Creek (1)				C				C	G	T									
5. Phelan (1)				C				C	G	T									
6. Phelan (1)				C				C	G	T									

The following are Informative sites for the Concatenated mtDNA haplotype bases 1-1299

[illegible]

The following are Informative sites for the Concatenated mtDNA haplotype bases 1300-1960

[illegible]

APPENDIX D

INPUT FILES

>Consensus_Sequence

GATATGCCACAACCTAAACCCATCTCCATGGTTTTTTATCTTGCTAATGACATG
ACTAATACTAATAATTTTTTATCTAAACAAAACCCTAAATATAATATTTCCAAA
CCCGCCAATTAACAACAATCAGAAAAAAAAGACCAAACACCTTGAACCTGA
CCATGATACTAAGCTTCTTTGATCAATTTTTAATCCCACAAACCCTAGGTATT
CCACTAATTCTAATTGCAATTATTATACCAACACTTATTATCTTAAGCTCTTCA
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>39._Mesquite_(1)

GATATGCCACAACCTAAATCCATCTCCATGGTTTCTTATCTTGCTAATGACATG
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TAAATGATAA

>40._Virgin_Delta_(1)

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CAAATCCTAACAGGACTATTTCTAGCCATACACTATACAGCTGACATTACATC
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TCCTAAAATGATAA

>3._Pioneer_Town_(1)

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CTTCCTTCTATTCTTATTTATTATGCCAACAACAGCAATCCTAGAGAACAAAC
TCCTAAAATGATAA

>4._Pioneer_Town_(1)

GATATGCCACAACCTAAACCCATCTCCATGGTTTCTTATCTTGCTAATGACATG
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AAAATGATAA

>2._Pioneer_Town_(1)

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AAATGATAA

>19._Muscoy_(1)

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AAAATGATAA

>17._Kenwood_(1)

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AAAATGATAA

>18._Verdemont_(1)

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AAGCATATGTCTTTGTTTTACTACTAAGATGACAATCATACGAAAATCCCACC
CAATAATCAAAATTGTAAACAGCTCATTTATTGACCTCCCAGCACCATCCAAC
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AAATCCTAACAGGACTATTTCTAGCCATACACTATACAGCTGACATTACATCA
GCCTTTTCATCCGTTGCTCACATCTGCCGAGATGTACAATATGGCTGACTTA
TCCGAAATATTCATGCCAACGGAGCCTCCATATTTTTTATCTGTATTTATCTC
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CATTGGAGTAATTCTACTACTATTAGTCATAGCAACGGCATTTCGTAGGATAC
GTCTTACCATGAGGACAAATATCATTTTGAGGGGCAACAGTTATTACTAATTT
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GGATTCTCCGTCGACAACGCAACACTAACCCGATTCTTTACCTTTCACTTTC
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AGGCGTACTCGCCTTACTTTTTTCAATCCTCATCCTCATACTAGTCCCAATAA
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CTGTAGAACACCCATTTATCATTATTGGACAACCTCGCCTCAATCACTTACTTC
CTTCTATTCTTATTTATTATGCCAACAACAGCAATCCTAGAGAACAACTCCT
AAAATGATAA

>20._Verdemont_(1)

GATATGCCACAACCTAAACCCATCTCCATGGTTTTTTATCTTGCTAATGACATG
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CCCGCCAATTAACAACAATCAGAAAAAAAAGACCAAACACCTTGAACCTGA
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CCACTAATTCTAATTGCAATTATTATACCAACACTTATTATCTTAAGCTCTTCA
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CTTTACAAAACAACCTTATTACACCTATCGGAATCTACGGGCATAAATGAGCA
TCAATACTTTTAGCCCTCACACTCCTTCTTATATCATTAAATTTAATAGGACTA
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CAACAGCGGCCTTTGTTTTAATACCATCAATAACACTAACAGCAACTGCAGC
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AAAATGATAA

>41. _Snow_Creek_(1)

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CTTTACAAAACAACCTATTACACCTATCGGAATCTACGGGCATAAATGAGCA
TCAATACTTTTAGCCCTCACACTCCTTCTTATATCATTAATTTAATAGGACTA
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AATCCTAACAGGACTATTTCTAGCCATACACTATACAGCTGACATTACATCA
GCCTTTTCATCCGTTGCTCACATCTGCCGAGATGTACAATATGGCTGACTTA
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CACATTGGACGAGGAATATACTATGGATCTTATATGTTTAAAGAAACATGAAA
CATTGGAGTAATTCTACTACTATTAGTCATAGCAACGGCATTTCGTAGGATAC
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AAAATGATAA

>24._Phelan_(1)

GATATGCCACAACCTAAACCCATCTCCATGGTTTTTTATCTTGCTAATGACATG
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CCCGCCAATTAACAACAATCAGAAAAAAAAGACCAAACACCTTGAACCTGA
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CTTTACAAAACAACCTTATTACACCTATCGGAATCTACGGGCATAAATGAGCA
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AAAATGATAA

>25._Phelan_(1)

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CTTCTATTCTTATTTATTATGCCAACAACAGCAATCCTAGAGAACAACTCCT
AAAATGATAA

>37._Kenwood_(1),_Verdemont_(1)

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CATTCATCATTCTTCTACTACTAACC GGACTTGAAATTGCTGTAGCAATAATT
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CCTTCTATTCTTATTTATTATACCAACAACAGCAATCCTAGAGAACAACCTCC
TAAATGATAA

>13._Verdemont_(1)

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CTTTACAAAACAACCTATTACACCTATCGGAATCTACGGGCATAAATGAGCA
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CAGTACCAATGTGAATAACAACGTACTAATTGGAATGCGAAACCAACCGAC
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ATCCTAATTATTATTGAACTATTAGTCTATTTATTTCGGCCACTTGCTCTTGG
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TCAACAGCGGCCTTTGTTTTAATACCATCAATAACACTAACAGCAACTGCAG
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CAAGCATATGTCTTTGTTTTACTACTAAGATGACAATCATACGAAAATCCAC
CCAATAATCAAAATTGTAAACAGCTCATTTATTGACCTCCCAGCACCATCCAA
CATTTTCAGCCTGATGAACTTTGGTTCACTACTGGGAATCTGCCTAATTATC
CAAATCCTAACAGGACTATTTCTAGCCATACACTATACAGCTGACATTACATC
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TAAATGATAA

>14._Muscoy_(1)

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CCTTCTATTCTTATTTATTATACCAACAACAGCAATCCTAGAGAACAACCTCC
TAAATGATAA

>31._Muscoy_(2)

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CTTTACAAAACAACCTTATTACACCTATCGGAATCTACGGGCATAAATGAGCA
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>34._Muscoy_(1)

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>27._Snow_Creek_(1)

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>28._Kenwood_(1)

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>26._Phelan_(1)

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>32._Snow_Creek_(1)

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>33._Phelan_(1)

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>29._Snow_Creek_(3)

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>30._Verdemont_(1)

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TACACACATCAAAACAACGAAGCACCTCCTTCCGACCAATATCTCAAACCAT
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AAAATGATAA

>35._Verdemont_(1)

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AAAATGATAA

>22._Pioneer_Town_(2)

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CCGAAATATTCATGCCAACGGAGCCTCCATATTTTTTATCTGTATTTATCTCC
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AAATGATAA

>15._Lucerne_(2)

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AAATGATAA

>16._Pioneer_Town_(3)

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AAATGATAA

>21. _Afton_Canyon_(1)

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AAAATGATAA

>36._Afton_Canyon_(1)

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AAAATGATAA

>38._Afton_Canyon_(1)_

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AAATGATAA

>23._Afton_Canyon_(1)

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ATTGTTCTACTAACCCTTACACTATTTTACCAAATCTACTAGGAGACCCAGA
AAACTTTTACCAGCAAATCCACTAGTAACCCCTCCACACATTAACCAGAA
TGATATTTCTATTTGCCTACGCCATCCTACGATCAATTCCAAACAAATTGGG
AGGCGTACTCGCCTTACTTTTTTCAATCCTCATCCTCATACTAGTACCAATAA
TACACACATCAAAACAACGAAGCACCTCCTTCCGGCCAATATCTCAAACCAT
ATTTTGACTTTTAATCTCAGATGTCCTCATTCTTACATGAATTGGAGGACAAC
CTGTAGAACACCCATTTATCATTATTGGACAACCTGCCTCAATCACTTACTTC
CTCCTATTCTTATTTATTATGCCAACAACAGCAATCCTAGAGAACAACTCCT
AAAATGATAA

>8. _Aster_Wash_(1)_

GATATGCCACAACCTAAACCCATCTCCATGGTTTCTTATCTTGCTAATGACATG
ACTAATACTAATAATTTTTTATCTAAACAAAACCTTAAATATAATGTTTCCAAA
CCCACCAATTAACAACAATCAGAAAAAAAAGACCAAACACCTTGAACCTGA
CCATGATACTAAGCTTCTTTGATCAATTTCTAATCCCACAAACCCCTAGGTATT
CCACTAATTCTAATTGCAATTATTATACCAACACTTATTATCTTAAGCTCTTCA
AACCGACTTATTTCAAATCGATTACTTACACTACAAGATTGGGCAACAAAAAC
CTTTACAAAACAACCTTATTATACCTATCGGAATTTACGGGCATAAATGAGCAT
CAATACTTTTtagccctcacactccttcttataatcattaaatttaataggactac
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agtaccaatgtgaataacaactgtactaattggaatgcgaaaccaaccaaca
gtatccctaggacacactactaccagaaggaactccaaccccaactaattccaa
tcctaattattattgaaaccattagtcattttattcgaccacttgctcttggc
gtccgactaaccgctaaccctaacagcagggcacctattaattcaactaattt
caacagcagcctttgTTTTAATACCATCAATAACACTAACAGCAACTGCAGC
ATTCATCATTCTTCTACTACTAACCggacttgaaatcgctgtagcaataattc
AAGCATACGTCTTTGTTTTACTACTGAGATGACAATCATACGAAAATCCCAC
CCAATAATCAAAATTGTAAACAGCTCATTcattgacctcccaacaccatccaa
catttcagcctgatgaaacttttgGATCACTACTGGGAATTTGCCTAATTATCC
AAATCCTAACAGGACTATTTCTAGCCATACACTATACAGCTGACATTACATCA
GCCTTTTCATCCGTTGCTCACATCTGCCGAGATGTTCAATATGGCTGACTTA
TCCGAAATATTCATGCCAACGGAGCCTCCATATTTTTTATCTGTATTTATCTC
CACATTGGACGAGGAATATACTATGGATCTTACATGTTTAAAGAAACATGAT
ACATTGGAGTAATTCTACTACTATTAGTCATAGCAACGGCATTCTGTAGGATA
CGTCTTACCATGAGGACAAATATCATTTTgAGGAGCAACAGTCATTACTAAT
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GAGGATTCTCCGTCGACAACGCAACACTAACCcggttctttacctttcactt
TCTCCTCCCATTcattattattggcatcaccataatacatctcctatTTTTACA
TGAAACAGGTTCAAACAACCCAACCTGGACTATCCTCAAACACAGACAAAGTT
CCATTTcaccCATATTTTTTCATACAAAGACCTCCTTGGAGCCCTACTACTAAT
CATTGTTCTACTAACCCTTGCACTATTTTCACCAAACCTACTAGGAGACCCA
GAAAACTTTTcaccAGCAAACCCACTAGTAACCCCTCCACACATTAAACCAG
AATGATATTTCTATTTGCCTACGCCATCCTACGATCAATTCCAAACAAATTG
GGAGGCGTACTCGCCCTACTTTTCTCAATCCTAATCCTCATACTAGTTCCAA
TAATACACACATCAAAACAACGAAGCACCTCCTTCCGACCGATATCTCAAC
CATATTTTGACTTTTAATCTCAGACGTCCTCATTCTTACATGAATTGGGGGAC
AACCTGTAGAACACCCATTTATTATTATTGGACAACCTTGCCTCAATCACTTAC
TTCCTTCTATTCTTATTcattataccaacaacagcaatactagagaacAACT
CCTAAAATGATAA

>45. _Snow_Creek_(1)

GATATGCCACAATTAAACCCATCTCCATGGTTTCTTATCTTGCTAATGACATG
ACTAATACTAATAATTTTTTATCTAAACAAAACCTTAAATATAATGTTTCCAAA
CCCACCAATTAACAACAATCAGAAAAAAAAGACCAAACACCTTGAACCTGA
CCATGATACTAAGCTTCTTTGATCAATTTCTAATCCCACAAACCCTAGGTATT
CCACTAATTCTAATTGCAATTATTATACCAACACTTATTATCTTAAGCTCTTCA
AACCGACTTATTTCAAATCGATTACTTACACTACAAGATTGGACAACAAAAAC
CTTTACAAAACAACCTTATTATACCTATCGGAATTTACGGGCATAAATGAGCAT
CAATACTTTTtagccctcacactccttcttatatcattaaatttaataggactac
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gtatccctaggacacactactaccagaaggaactccaacccccactaattccaa
tcctaattattattgaaaccattagtctatTTATTGACCACCTTGCTCTTGGC
GTCCGACTAACCGCTAACCTAACAGCAGGACACCTATTAATTCAACTAATTT
CAACAGCGGCCTTTGTTTTAATACCATCAATAACACTAACAGCAACTGCAGC
ATTCATCATTCTTCTACTACTAACC GGACTTGAAATCGCTGTAGCAATAATTC
AAGCATACGTCTTTGTTTTACTACTAAGATGACAATCATACGAAAATCCCACC
CAATAATCAAAATTGTAAACAGCTCATTGACCTCCCAGCACCATCCAA
CATTTGAGCCTGATGAACTTTGGATCACTACTGGGAATTTGCCTAATTATCC
AAATCCTAACAGGACTATTTCTAGCCATACACTATACAGCTGACATTACATCA
GCCTTTTCATCCGTTGCTCACATCTGCCGAGATGTTCAATATGGCTGACTTA
TCCGAAATATTCATGCCAACGGAGCCTCCATATTTTTTATCTGTATTTATCTC
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CGTCTTACCATGAGGACAAATATCATTTTGAGGAGCAACAGTCATTACTAAT
TTACTATCAGCTATTCCTTACGTAGGAACAACCCTAGTAGAATGAATCTGAG
GAGGATTCTCCGTCGACAACGCAACACTAACCCGATTCTTTACCTTTCACTT
TCTCCTCCCATTCATTATTATTGGCATCACCATAATACATCTCCTATTTTTACA
TGAAACAGGTTCAAACAACCCAACTGGACTATCCTCAAACACAGACAAAGTT
CCATTTCACCCATATTTTTTCATACAAAGACCTCCTTGGAGCCCTACTACTAAT
CATTGTTCTACTAACCCTTGCACTATTTTCACCAAACCTACTAGGAGACCCA
GAAAACTTTTACCAGCAAACCCACTAGTAACCCCTCCACACATTAACCAG
AATGATATTTCTATTTGCCTACGCCATCCTACGATCAATTCCAAACAAATTG
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TAATACACACATCAAAACAACGAAGCACCTCCTTCCGACCAATATCTCAAAC
CATATTTTGACTTTTAATCTCAGACGTCTCATTCTTACATGAATTGGAGGAC
AACCTGTAGAACACCCATTTATTATTATTGGACAACCTTGCCTCAATCATTTAC
TTCCTTCTATTCTTATTATTATACCAACAACAGCAATACTAGAGAACAACCT
CCTAAAATGATAA

>42._Phelan_(1)

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ACTAATACTAATAATTTTTTATCTAAACAAAACCTTAAATATAATGTTTCCAAA
CCCACCAATTAACAACAATCAGAAAAAAAAGACCAAACACCTTGAACCTGA
CCATGATACTAAGCTTCTTTGATCAATTTCTAATCCCACAAACCCTAGGTATT
CCACTAATTCTAATTGCAATTATTATACCAACACTTATTATCTTAAGCTCTTCA
AACCGACTTATTTCAAATCGATTACTTACACTACAAGATTGGGCAACAAAAAC
CTTTACAAAACAACCTTATTATACCTATCGGAATTTACGGGCATAAATGAGCAT
CAATACTTTTtagccctcacactccttcttataatcattaaatttaataggactac
taccatatacatTTTACACCAACAACACAACGTCAATAAACATGGCACTAGC
AGTACCAATGTGAATAACAACGTACTAATTGGAATGCGAAACCAACCAACA
GTATCCCTAGGACACCTACTACCAGAAGGAACTCCAACCCCACTAATTCCAA
TCCTAATTATTATTGAAACCATTAGTCTATTTATTGACCACTTGCTCTTGGC
GTCCGACTAACCGCTAACCTAACAGCAGGACACCTATTAATTCAACTAATTT
CAACAGCGGCCTTTGTTTTAATACCATCAATAACACTAACAGCAACTACAGC
ATTTATTATTCTTCTACTACTAACC GGACTTGAAATCGCTGTAGCAATAATTC
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CAATAATCAAAATTGTAAACAGCTCATTGACCTCCCAGCACCATCCAA
CATTTGAGCCTGATGAACTTTGGATCACTACTGGGAATTTGCCTAATTATCC
AAATCCTAACAGGACTATTTCTAGCCATACACTATACAGCTGACATTACATCA
GCCTTTTCATCCGTTGCTCACATCTGCCGAGATGTTCAATATGGCTGACTTA
TCCGAAATATTCATGCCAACGGAGCCTCCATATTTTTTATCTGTATTTATCTC
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CATATTTTGACTTTTAATCTCAGACGTCTCATTCTTACATGAATTGGGGGAC
AACCTGTAGAACACCCATTTATTATTATTGGACAACCTTGCCTCAATCACTTAC
TTCCTTCTATTCTTATTATTATACCAACAACAGCAATACTAGAAAACAACT
CCTAAAATGATAA

>43._Phelan_(1)

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CCACTAATTCTAATTGCAATTATTATACCAACACTTATTATCTTAAGCTCTTCA
AACCGACTTATTTCAAATCGATTACTTACACTACAAGATTGGGCAACAAAAAC
CTTTACAAAACAACCTTATTATACCTATCGGAATTTACGGGCATAAATGAGCAT
CAATACTTTTtagccctcacactccttcttatatcattaaatttaataggactac
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agtaccaatgtgaataacaactgtactaattggaatgcgaaaccaaccaaca
gtatccctaggacacactactaccagaaggaactccaacccccactaattccaa
tcctaattattattgaaaccattagtcattttattcgaccacttgctcttggc
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caacagcggcctttgTTTTAATACCATCAATAACACTAACAGCAACTACAGC
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CATTTCAGCCTGATGAAACTTTGGATCACTACTGGGAATTTGCCTAATTATCC
AAATCCTAACAGGACTATTTCTAGCCATACACTATACAGCTGACATTACATCA
GCCTTTTCATCCGTTGCTCACATCTGCCGAGATGTTCAATATGGCTGACTTA
TCCGAAATATTCATGCCAACGGAGCCTCCATATTTTTTATCTGTATTTATCTC
CACATTGGACGAGGAATATACTATGGATCTTACATGTTCAAAGAAACATGAA
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CGTCTTACCATGAGGACAAATATCATTTTgAGGAGCAACAGTCATTACTAAT
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GAGGATTCTCCGTCGACAACGCAACACTAACCCGATTCTTTACCTTTCACTT
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CCATTTcACCCATATTTTTTCATACAAAGACCTCCTTGGAGCCCTACTACTAAT
CATTGTTCTACTAACCCTTGCACTATTTTCACCAAACCTACTAGGAGACCCA
GAAAACTTTTcACCAGCAAACCCACTAGTAACCCCTCCACACATTAACCAG
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TAATACACACATCAAAACAACGAAGCACCTCCTTCCGACCAATATCTCAAAC
CATATTTTGACTTTTAATCTCAGACGTCTCATTCTTACATGAATTGGGGGAC
AACCTGTAGAACACCCATTTATTATTATTGGACAACCTTGCCTCAATCACTTAC
TTCCTTCTATTCTTATTcATTATACCAACAACAGCAATACTAGAAAACAACT
CCTAAAATGATAA

>44._Phelan_(1)

GATATGCCACAATTAAACCCAGCTCCATGGTTTCTTATCTTGCTAATGACATG
ACTAATACTAATAATTTTTTATCTAAACAAAACCTTAAATATAATGTTTCCAAA
CCCACCAATTAAACAACAATCAGAAAAAAAAGACCAAACACCTTGAACCTGA
CCATGATACTAAGCTTCTTTGATCAATTTCTAATCCCACAAACCTAGGTATT
CCACTAATTCTAATTGCAATTATTATACCAACACTTATTATCTTAAGCTCTTCA
AACCGACTTATTTCAAATCGATTACTTACACTACAAGATTGGGCAACAAAAAC
CTTTACAAAACAACCTTATTATACCTATCGGAATTTACGGGCATAAATGAGCAT
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agtaccaatgtgaataacaactgtactaattggaatgcgaaaccaaccaaca
gtatccctaggacacactactaccagaaggaactccaaccccaactaattccaa
tcctaattattattgaaaccattagtctatTTATTGACCACTTGCTCTTGGC
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CAACAGCGGCCTTTGTTTTAATACCATCAATAACACTAACAGCAACTACAGC
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CCAATAATCAAAATTGTAAACAGCTCATTGACCTCCCAGCACCATCCA
ACATTTTCAGCCTGATGAAACTTTGGATCACTACTGGGAATTTGCCTAATTATC
CAAATCCTAACAGGACTATTTCTAGCCATACACTATACAGCTGACATTACATC
AGCCTTTTTCATCCGTTGCTCACATCTGCCGAGATGTTCAATATGGCTGACTT
ATCCGAAATATTCATGCCAACGGAGCCTCCATATTTTTTATCTGTATTTATCT
CCACATTGGACGAGGAATATACTATGGATCTTACATGTTCAAAGAAACATGA
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GAAAACTTTTACCAGCAAACCCCACTAGTAACCCCTCCACACATTAACCAG
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AACCTGTAGAACACCCATTTATTATTATTGGACAACCTTGCCTCAATCACTTAC
TTCCTTCTATTCTTATTCAATTATACCAACAACAGCAATACTAGAAAACAACT
CCTAAAATGATAA

>46._Snow_Creek_(1)

GATATGCCACAATTAAACCCATCTCCATGGTTTCTTATCTTGCTAATGACATG
ACTAATACTAATAATTTTTTATCTAAACAAAACCTTAAATATAATGTTTCCAAA
CCCACCAATTAACAACAATCAGAAAAAAAAGACCAAACACCTTGAACCTGA
CCATGATACTAAGCTTCTTTGATCAATTTCTAATCCCACAAACCCTAGGTATT
CCACTAATTCTAATTGCAATTATTATACCAACACTTATTATCTTAAGCTCTTCA
AACCGACTTATTTCAAATCGATTACTTACACTACAAGATTGGGCAACAAAAAC
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CAATACTTTTAGCCCTCACACTCCTTCTTATATCATTAAATTTAATAGGACTAC
TACCATATACATTTACACCAACAACACAACCTGTCAATAAACATGGCACTAGC
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GTATCCCTAGGACACCTACTACCAGAAGGAACTCCAACCCCACTAATTCCAA
TCCTAATTATTATTGAAACCATTAGTCTATTTATTGACCACTTGCTCTTGGC
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CAACAGCGGCCTTTGTTTTAATACCATCAATAACACTAACAGCAACTACAGC
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AAATCCTAACAGGACTATTTCTAGCCATACATTATACAGCTGACATTACATCA
GCCTTTTCATCCGTTGCTCACATCTGCCGAGATGTTCAATATGGCTGACTTA
TCCGAAATATTCATGCCAACGGAGCCTCCATATTTTTTATCTGTATTTATCTC
CACATTGGACGAGGAATATACTATGGATCTTACATGTTTAAAGAAACATGAA
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CGTCTTACCATGAGGACAAATATCATTTTGAGGAGCAACAGTCATTACTAAT
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GAGGATTCTCCGTCGACAACGCAACACTAACCCGATTCTTTACCTTTCACTT
TCTCCTCCCATTCATTATTATTGGCATCACCATAATACATCTCCTATTTTTACA
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TAATACACACATCAAAACAACGAAGCACCTCCTTCCGACCAATATCTCAAAC
CATATTTTGACTTTTAATCTCAGACGTCCTCATTCTTACATGAATTGGGGGAC
AACCTGTAGAACACCCATTTATTATTATTGGACAACCTTGCCTCAATCATTTAC
TTCCTTCTATTCTTATTTCATTATACCAACAACAGCAATACTAGAAAACAACT
CCTAAAATGATAA

>47._Pioneer_Town_(1)

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CCACTAATTCTAATTGCAATTATTATACCAACACTTATTATCTTAAGCTCTTCA
AACCGACTTATTTCAAATCGATTACTTACACTACAAGATTGGGCAACAAAAAC
CTTTACAAAACAACCTTATTATACCTATCGGAATTTACGGGCATAAATGAGCAT
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TACCATATACATTTACACCAACAACACAACCTGTCAATAAACATGGCACTAGC
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GTATCCCTAGGACACCTACTACCAGAAGGAACTCCAACCCCACTAATTCCAA
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TAATACACACATCAAAACAACGAAGCACCTCCTTTGACCAATATCTCAAAC
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AACCTGTAGAACACCCATTTATTATTATTGGACAACCTTGCCTCAATCATTTAC
TTCCTTCTATTCTTATTATTATACCAACAACAGCAATACTAGAAAACAACT
CCTAAAATGATAA

>11._Aster_Wash_(1)

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CTTTACAAAACAACCTTATTATACCTATCGGAATTTACGGGCATAAATGAGCAT
CAATACTTTTtagccctcacactccttcttataatcattaaatttaataggactac
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gtatccctaggacacactactaccagaaggaactccaacccccactaattccaa
tcctaattattattgaaaccattagtctatTTATTTCGACCACTTGCTCTTGGC
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AAGCATACGTCTTTGTTTTACTACTAAGATGACAATCATACGAAAATCCCACC
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CATTTTCAGCCTGATGAACTTTGGATCACTACTGGGAATTTGCCTAATTATCC
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TCCGAAATATTCATGCCAACGGAGCCTCCATATTTTTTATCTGTATTTATCTC
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CATATTTTGACTTTTAATCTCAGACGTCTCATTCTTACATGAATTGGGGGAC
AACCTGTAGAACACCCATTTATTATTATTGGACAACCTTGCCTCAATCACTTAC
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>12._Aster_Wash_(1)

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>9. Indian_Wash_(1)

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>10._Indian_Wash_(1)

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>7._Virgin_Delta_(1)

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>1. _Snow_Creek_(1)

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>5._Phelan_(1)

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>6._Phelan_(1)

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MR BAYES INPUT FILE

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