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Are corridors effective? A genetic study of Texas Spiny Lizard populations in urban parks of San Antonio

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Abstract

Habitat fragmentation results in smaller, more isolated populations, which experience a higher risk of extinction due to inbreeding, genetic drift, and environmental catastrophes. Wildlife populations in urban areas are frequently fragmented, but corridors connecting these areas may help conserve urban populations. In theory, corridors allow genetic diversity and relatedness of populations to be maintained through gene flow, increasing the overall fitness of otherwise isolated populations. I studied the population genetics of the Texas Spiny Lizard (*Sceloporus olivaceus)* in San Antonio, Texas to determine whether corridors impact the genetic diversity or genetic relatedness of lizard populations. Genetic diversity was surveyed using six microsatellite loci derived from the Eastern Fence Lizard (*Sceloporus undulatus*). I compared genetic diversity and relatedness between isolated, corridor, and rural localities. Individuals within a population were more closely related to one another than to individuals in any other population. There was a trend of isolation by distance over all localities ($P < 0.01$), but not among only the urban localities ($P = 0.67$). The difference in average pairwise F_{ST} for isolated localities (any pair not connected by a corridor) versus corridor localities (any pair connected by a corridor) was not statistically significant ($P = 0.11$). The difference in average H_o of all corridor localities versus all isolated localities was not statistically significant ($P = 0.11$). The samples most likely represented two clusters, based on analysis with STRUCTURE and TESS. The samples from the rural population formed one cluster, and the urban samples formed the other cluster, according to TESS. My results suggest that genetic relatedness may be higher between populations connected by a corridor, but genetic diversity is similar, when compared to isolated populations. This study demonstrates that common species, such as the Texas Spiny Lizard, can be useful model organisms for testing conservation principles in urban environments.

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Introduction

Habitat fragmentation of large areas leads to smaller, more isolated populations. Fragmented populations, because of their smaller size, are subject to inbreeding depression and genetic drift, which reduces genetic diversity and results in populations that are less adaptable to environmental change and more vulnerable to extinction (Wright 1932, Lande 1998, Keller & Waller 2002, Traill et al. 2010). The long-term survival of small populations is critical for conservation efforts, but management solutions are complex and species-specific in many cases. Soulé and Simberloff (1986) suggested that long-term survival of a population could be predicted by a minimum viable population size, but genetic diversity is also important because it allows for evolutionary adaptability in a changing environment (Wright 1932, Pease et al. 1989, Traill et al. 2010). Thus, maintenance of genetic diversity is critical for conservation efforts.

Due to habitat fragmentation, many remaining habitats and wildlife reserves are isolated and effectively islands, so conservation of these habitats can be informed by the theory of island biogeography. MacArthur and Wilson (1967) developed the theory of island biogeography that explains species richness of islands based on island size (bigger islands have more species) and isolation from mainland sources (more isolated islands have fewer species). However, controversy developed over how the theory should be applied to wildlife reserve design. For example, some suggest a single large reserve will conserve more species than several small reserves (Simberloff & Abele 1976), but others suggest that several small reserves will conserve more species than a single large one (Diamond 1975, Gilpin & Diamond 1980). This is known as the SLOSS (single large or several small) debate.

However, much of the debate is largely based on theory and empirical evidence is rare. Both sides of the argument express the need for more empirical data (Simberloff & Abele 1976,

Järvinen 1982, Willis 1984, Saunders et al. 1991). Some suggest that in reality neither option is ideal, as the specific attributes of the environment and species of concern will determine whether a single large or several small reserves is best (Higgs & Usher 1980, Gilpin & Diamond 1980, Järvinen 1982). The SLOSS debate developed the importance of habitat connectivity (Keller & Waller 2002), which may be more indicative of long-term population viability than habitat size. Population modeling has demonstrated that any connection between two isolated populations results in longer population persistence and larger population size than with no connection at all (Henein & Merriam 1990).

Corridors, defined as linear stretches of habitat that connect larger, otherwise isolated patches of habitat, are a possible solution to population isolation. In theory, corridors allow migration and gene flow between populations, creating a meta-population that maintains genetic diversity (Fahrig & Merriam 1985, Labaree 1997). However, corridor effectiveness depends on the species of focus, the particular environment (Beier & Noss 1998), and the contrast between the corridor habitat and the surrounding environment (Rosenberg et al. 1997). The greater the habitat quality of the corridor compared to the habitat quality of the surrounding environment, the more useful and important the corridor is likely to be (Rosenberg et al. 1997).

There may be negative effects of corridors as well, including the spread of infectious diseases (Simberloff & Cox 1987), parasites (Yahner 1988), and invasive species (Resasco et al. 2014). However, invasive species are typically invasive because of their dispersal ability, and it is likely that they can disperse through a matrix of habitat whether or not corridors are present (Noss & Cooperrider 1994). Increased edge habitat is another possible negative effect of corridors (Willis 1984, Yahner 1988, Harris 1988, Hobbs 1992, Rosenberg et al. 1997). Edge habitat can increase an animal's exposure to humans and other predators (Willis 1984,

Simberloff & Cox 1987, Yahner 1988), and is often lower quality habitat that may cause a corridor to act as a "sink" (Hobbs 1992, Lande 1998). Sink populations, where the death rate exceeds the birth rate, are only maintained by constant immigration from a source population, where the birth rate exceeds the death rate. Thus, sink populations may possess less evolutionary value than source populations (Pulliam 1988). A corridor should be wide enough to allow breeding and population survival within the corridor, particularly for species that only disperse short distances (Simberloff et al. 1992). Corridor habitat quality must also be considered, otherwise corridors may act as sinks instead of important features of connectivity (Henein & Merriam 1990).

While there is a need for more studies on the negative effects of corridors, the magnitude of the benefits likely outweighs the possible costs (Beier & Noss 1998, Resasco et al. 2014). Studies showing corridor effectiveness include: increased population connectivity for voles (Mech & Hallett 2001), increased genetic diversity and gene flow in populations of butterflies (Wells et al. 2009), increased connectedness of two populations of Florida black bears (Dixon et al. 2006), increased plant species richness (Damschen et al. 2006), and increased plant pollination and seed dispersal (Tewksbury et al. 2002). Corridors may be especially important for species that have small home ranges and disperse short distances; however, this requires the corridor to contain habitat with high enough quality to maintain healthy multi-generational populations within the corridor (Simberloff et al. 1992, Barrows et al. 2011).

Corridors exist naturally, but they have also been developed throughout the world as a conservation technique, most notably with large mammals (Dutta et al. 2013, Joshi et al. 2013). There have been many studies investigating corridors, many of which conclude they are effective conservation methods (Gilbert-Norton et al. 2010). Corridor effectiveness for a single species in

a particular environment cannot be generalized to all species, so there is still a need for more studies on other species of interest and in different environments (Hobbs 1992, Rosenberg et al. 1997, Gilbert-Norton et al. 2010). In particular, urban environments are grossly understudied in terms of corridors (Collins et al. 2000, Miller & Hobbs 2002).

Urban environments, and the alarming rate at which they are expanding (United Nations 2014), provide additional challenges for conservation. Relative abundance of species, species richness, and species diversity are lower in urban environments for a variety of taxa (Gomes et al. 2011, McKinney 2002, Pauchard et al. 2006). Often, non-native species are introduced and replace native species, homogenizing the environment (McKinney 2002, Pauchard et al. 2006). One of the major problems with urbanization is habitat destruction and subsequent fragmentation of the remaining habitats (Medley et al. 1995, Wilcove et al. 1998, Collins et al. 2000). A natural environment may contain areas of lower quality habitat that act as small divisions between populations, but a dense urban landscape provides a much larger barrier to dispersal for most species (Vignoli et al. 2009). For example, freeways have been shown to genetically divide populations of bobcats (Serieys et al. 2014).

How can habitat with healthy populations of animals be maintained while still allowing human development? Urban parks and natural areas have long been recognized as providing critical habitat for local species, as well as providing for healthy, prosperous cities (National Park Service 1995). While the SLOSS debate may be applicable when establishing wildlife reserves, urban development often leaves conservationists with little choice of method (Rosenberg et al. 1997). Thus, corridors may provide a "win-win" solution in urban environments, providing connectivity to maintain healthy populations of native species, while also providing linear park space that has recreational value (Rosenberg et al. 1997). Parks and gardens are likely important

units of ecological conservation in an urban environment (Goddard et al. 2010), and have been shown to be possible corridors between populations of mice in New York City (Munshi-South 2012).

Unfortunately, many studies lack proper design and controls to draw strong conclusions about corridor effectiveness. Several are done in artificial or highly manipulated landscapes, reducing the applicability of their conclusions to conservation of natural populations (Beier & Noss 1998, Mech & Hallett 2001). Also, some do not test if corridors influence the genetic diversity of the populations (Traill et al. 2010). While individuals may be found in the corridor, or found to migrate between populations connected by a corridor, there is still the need for evidence that gene flow occurs as a result. Properly designed, large-scale landscape studies are needed to test the effectiveness of corridors (Gilbert-Norton et al. 2010).

In this study, I tested the effectiveness of corridors between parks by analyzing the genetic structure and diversity of the Texas Spiny Lizard (*Sceloporus olivaceus*) in San Antonio, Texas. This species is arboreal and limited to areas with enough trees to provide quality habitat, which are often not found in dense urban matrix (Blair 1960). San Antonio has recently set aside linear parks that act as corridors between otherwise isolated parks (see http://www.sanantonioriver.org/), providing replication of site type (isolated and corridor). I took advantage of these linear parks that connect populations to test the following in the Texas Spiny Lizard: (1) geographically closer populations are more closely related genetically than populations further apart, (2) individuals within the same population are more closely related to one another than to individuals in any other population, (3) rural populations have more genetic diversity than corridor populations, which in turn have more genetic diversity than isolated populations, and (4) genetic relatedness between isolated populations is lower than similarly

distanced populations connected by a corridor. By comparing the population genetics between isolated, corridor, and urban populations I will be able to determine whether the linear parks in San Antonio act as effective corridors for Texas Spiny Lizards.

Materials and Methods

Study Species

The Texas Spiny Lizard (*Sceloporus olivaceus*) is a common lizard with a range extending from Northern Mexico north through central Texas to Oklahoma (Blair 1960). The following is a summary adapted from Blair (1960). The Texas Spiny Lizard is an arboreal species and is reproductively active from late April through early October. Females attain reproductive size and coloration at about one year of age. Most females only produce one clutch with an average of 11.3 eggs in their first year and an average of four clutches per year, with about 20 eggs per clutch, in the following years. Hatching occurs 43-83 days after laying. Dispersal typically occurs in juveniles, with males dispersing an average of 75 m and females dispersing an average of 50 m. Blair (1960) also found that dispersal direction is dependent upon availability of suitable habitat. The lifespan of *S. olivaceus* is approximately two to five years. Adults establish home territories that remain relatively constant in size and location throughout their life, with adult dispersal being rare.

Sample Collection

I caught Texas Spiny Lizards (*Sceloporus olivaceus*) at five sites in and around San Antonio, Texas. These included two urban isolated sites: Headwaters Sanctuary (HW) and Phil Hardberger Park (PH), two urban corridor sites: Salado Creek (SC) and Leon Creek (LC), and one rural site: private property in Hays County (HC) (Fig. 1). I further divided each corridor site into localities based upon natural breaks in my collections within each corridor system. I established three localities in Salado Creek, the first division as Wetmore Road and the second division as Loop 410. The most northern locality, Salado Creek North, contains McAllister Park,

the most southern locality, Salado Creek South, contains Tobin Park, and the central locality, Salado Creek Central, contains Lady Bird Johnson Park. I established two localities in Leon Creek, the division lying just west of Bandera Road.

I captured lizards from May through September in 2013 and 2014. I captured, by noose or hand, a total of 224 lizards, with 25 from HW, 44 from PH, 89 from SC, 45 from LC, and 21 from HC. I obtained DNA from 1-2 cm of tail-tip collected from each individual, stored in 100% ethanol in the field, and stored at -80°C in the laboratory until DNA extraction. I also clipped the third toe on the back right foot of each lizard to allow me to determine if an individual had previously been captured and sampled, preventing me from resampling a recaptured individual. I obtained GPS information at the site of capture for each individual using a Trimble GeoExplorer XT 2008 Series. I differentially corrected locations after collection to sub-meter accuracy using Trimble TerraSync software. I recorded all geographic data using the WGS 1984 datum.

Molecular Methods

I digested tail-tip samples in 700 µL lysis buffer (50 mM Tris HCl pH 8.0, 50 mM EDTA pH 8.0, 1% SDS, 100 mM NaCl, 1% 2-mercaptoethanol) with 15 µL proteinase K (10 mg/mL) overnight at 55°C in a shaking incubator. I extracted and isolated DNA from each sample using equilibrated phenol and alcohol precipitation as reported in Ribble (1991). I suspended DNA samples in 100 µL 1X TE buffer and quantified them using a Nanodrop ND-1000 Spectrophotometer. Samples were diluted to between 75 and 150 ng/µL and stored at 4°C.

I obtained seven untagged primer pairs (Sigma) designed for the Eastern Fence Lizard (*Sceloporus undulatus*) microsatellite loci by Lance et al. (2009) and optimized their annealing temperatures for the Texas Spiny Lizard (*Sceloporus olivaceus*) (Table 1). I performed PCR with

each primer pair using a 55-64°C temperature gradient for annealing temperatures. I determined the annealing temperature for each primer pair to be the highest temperature that yielded PCR product clearly visible on an electrophoresis gel.

Optimized PCR reactions were performed using an Eppendorf thermal cycler in a total reaction volume of 20 µL containing 10 µL *Taq* 2X Master Mix (New England BioLabs), 0.5 µL 100µM forward primer, 0.5 µL100 µM reverse primer, 1 µL working concentration template DNA, and 8 µL sterile diH_2O. The PCR conditions for all microsatellite loci were as follows: (1) Initial denaturation, 95°C for 30 sec, followed by (2) 40 cycles of 30 sec at 96°C, 30 sec at the annealing temperature (Table 1), and 30 sec at 78°C, and (3) final extension, 5 min at 78°C. I ran all PCR products in 0.8% agarose gel with ethidium bromide and viewed with Image Lab Software Version 4.1 and a Bio-Rad Gel Doc EZ Imager to verify PCR product was visible and the expected length.

I performed PCR on all samples with all seven primer pairs using their respective annealing temperature (Table 1), fluorescently tagged forward primers, and untagged reverse primers (Sigma). In a few cases, individuals showed no PCR product on the gel, so I re-optimized the primers and ran a second round of PCR using a second annealing temperature (Table 1). Samples that still showed no amplification were re-isolated using QIAamp DNA Micro Kit (Qiagen) following the manufacturer's instructions after the lysis steps, and I performed PCR on these samples using a second annealing temperature (Table 1). I sent each sample to the University of Texas at Austin ICMB Core Facility to be genotyped using capillary electrophoresis on a LifeTech – Applied Biosystems 3730 Sequencer. I manually scored the genotype of each sample using Peak Scanner Software 2 (Applied Biosystems). I removed locus Scun6 from the study due to poor PCR amplification. Only samples that were genotyped for at

least three out of the six remaining loci were used in this study. I removed from further study samples that failed to be genotyped at more than three of the six remaining loci due to poor PCR amplification.

Data Analysis

I tested for genotyping error, the presence of null alleles, scoring errors, and large allele dropout using MICRO-CHECKER (Van Oosterhout et al. 2004). I used CONVERT (Glaubitz 2004) to convert data to GENEPOP format. I calculated locality summary statistics and pairwise F_{ST}, and tested linkage disequilibrium and Hardy-Weinberg equilibrium using GENEPOP (Raymond & Rousset 1995, Rousset 2008). I used GenAlEx 6.5 (Peakall & Smouse 2006, Peakall & Smouse 2012) to calculate the genetic distance between each sample pair. I then used this data to construct a UPGMA phenogram with the linkage and dendrogram functions in MATLAB (The MathWorks). I accepted statistical significance at $P < 0.05$.

I determined population structure using STRUCTURE (Pritchard et al. 2000). I used the admixture model, with no prior population information, correlated allele frequencies with alpha interpreted from the data (default), 5,000 burn-in iterations, 10,000 run iterations, and ten runs per K for K = 1-10. I used STRUCTURE HARVESTER (Earl 2012) for the Delta K analysis, which helps determine the most likely number of clusters. Then I used CLUMPP (Jakobsson & Rosenberg 2007) to average and account for label switching across runs, and DISTRUCT (Rosenberg 2004) to visualize the results. The cluster assignments in this analysis do not incorporate geographical distribution of samples.

I also analyzed population structure using TESS (Chen et al. 2007, Durand et al. 2009), which is a program similar to STRUCTURE, but it also incorporates the geographic coordinates

of the samples. I used the CAR admixture model, interaction parameter of 0.6 (default), 10,000 burn-in sweeps, 60,000 total sweeps, and ten runs per K for K = 2-10. I averaged the DIC across the ten runs performed at each K value to determine the most likely number of clusters.

Results

This study included a total of 224 lizards, but some were removed due to genotyping error. The genetic analysis included 159 lizards, with 15 from HW, 21 from PH, 66 from SC, 37 from LC, and 20 from HC. Of these 43 samples were missing some genotype data, with 31 samples missing one locus, nine samples missing two loci, and three samples missing three loci. Genotype data were missing for zero samples (0%) at Scun2, one sample (0.5%) at Scun3, two samples (1.3%) at Scun5, 16 samples (10.1%) at Scun13, 35 samples (22.0%) at Scun15, and 3 samples (1.9%) at Scun16.

There were no genotyping errors due to stuttering or large allele dropout for any loci according to MICRO-CHECKER. Possible null alleles were detected at locus Scun16 ($P < 0.01$), but no null alleles were detected at any of the other loci (all $P > 0.05$). Linkage disequilibrium was detected for Scun3 and Scun15 by GENEPOP ($P < 0.05$). All other loci pairs showed no evidence of linkage disequilibrium (all $P > 0.05$). All loci showed genetic variability over all localities (Table 2) and within each locality (Table 3).

There was a trend of isolation by distance over all localities (Fig. 2; $R^2 = 0.5868$, df = 27, $P < 0.01$). However, this was driven by urban localities paired with the single rural population (HC). When I removed the pairs with the rural population, the trend was lost (Fig. 3; $R^2 = 0.0097$, df = 20, $P = 0.67$). Thus, among only the urban localities there was no trend of isolation by distance. Pairwise geographic distances and F_{ST} values are given in Table 4.

Average pairwise F_{ST} for isolated localities (any pair not connected by a corridor, excluding HC), were greater than average pairwise F_{ST} for corridor localities (any pair connected by a corridor; Fig. 4). However, this difference was not statistically significant ($F = 4.87$, $P = 0.110$). The pairwise F_{ST} value between the two isolated localities, HW and PH, was much

higher than the pairwise F_{ST} value between the two ends of SC, Salado Creek North and Salado Creek South, which are similarly distanced (Fig. 5). The pairwise F_{ST} values between all localities ranged from -0.011 to 0.094, and geographic distance ranged from 2.47 to 68.87 km.

Individuals within a population were more closely related to one another than to individuals in any other population, as shown by the UPGMA phenogram constructed in MATLAB (Fig. 6). These similarities also showed that individuals within a locality were more closely related to individuals in a locality within the same corridor site than to any other site.

When average observed heterozygosity (H_o) of a locality differed significantly from the average expected heterozygosity (H_e), H_o was always lower than H_e (Table 5). The H_o in the rural locality (HC) was greater than the average H_o of corridor localities and the average H_o of all isolated localities (Fig. 7). The average H_o of all corridor localities was lower than the average H_o of all isolated localities. However, the difference was not statistically significant ($F = 4.25$, $P = 0.108$).

The samples most likely represented two clusters, indicated by the STRUCTURE Delta K analysis with STRUCTURE HARVESTER. However, individuals within the same locality did not tend to belong to the same cluster, so the clusters did not correspond with any geographical pattern (Fig. 8). Similarly, the TESS DIC averages across ten runs at each K value indicated the samples most likely represented two clusters. While this was similar to the STRUCTURE result, the cluster diagram (Fig. 9) and tessellation (Fig. 10) indicated there was a geographical relationship between the clusters. Individuals within the same locality tended to cluster together. The samples from the rural population (HC) formed one cluster, and the urban samples formed the other cluster.

Discussion

Overall, I found mixed support for corridor effectiveness. While the results suggested that genetic relatedness between populations is higher in corridor populations compared to isolated populations, they did not indicate that genetic diversity is higher in corridor populations than in isolated populations. The lack of isolation by distance within the urban localities suggests any population structure is not due to geographic distance. The results from pairwise F_{ST} values and the relatedness of individuals within a locality compared to individuals in other localities support the idea that genetic population structure could be correlated with corridor presence. However, the heterozygosity results suggest that the urban localities were less genetically diverse than the rural locality, regardless of whether they were isolated or connected by a corridor. My results indicate that for urban populations of Texas Spiny Lizards in San Antonio parks, populations connected by corridors may have increased relatedness, but similar genetic diversity, when compared to isolated populations. Increased relatedness could be caused by geographic barriers in the urban environment that influence genetic population structure. Similar genetic diversity in corridor and isolated localities could be caused by populations of Texas Spiny Lizards within the urban environment that may share gene flow with the parks.

Munshi-South (2012) found slightly higher pairwise F_{ST} values (0.033 – 0.145) for white-footed mice, looking at similar distanced populations (0.83 – 24.28 km). However, these populations were located in New York City, where urbanization is more developed and there is less green space than in San Antonio. Thus, the greater habitat destruction of New York City is expected to cause greater differentiation than the lower level of habitat fragmentation in San Antonio. Hutchison and Templeton (1999) found much higher pairwise F_{ST} values between some

populations of collared lizards (0 – 0.8872), but these populations were typically much further apart (0.25 – 405 km) than the populations in my study.

I predicted that populations closer to one another would be more closely related than populations further apart (Hypothesis 1). While the pairwise F_{ST} results indicated this trend of isolation by distance was present overall, it was driven by the rural (HC) locality. The trend was lost when I removed this locality, indicating the localities in the urban environment were not isolated by distance. Barriers to dispersal present in an urban environment, such as highways or buildings, could prevent the random dispersal necessary for isolation by distance to develop. Hutchison and Templeton (1999) found a similar pattern of isolation by distance in their study of Collared Lizards. Across large distances of up to 405 miles, they found isolation by distance, but in a smaller, more fragmented region with distances less than 60 miles, they found no isolation by distance. They also reported the region with no isolation by distance was the most heavily fragmented, suggesting the lack of isolation by distance shown in my study could be due to heavy fragmentation of the urban environment.

Since I found no isolation by distance between the urban localities, I expected genetic relatedness between two populations connected by a corridor to be greater than between two similarly distanced populations that are isolated from one another (Hypothesis 4). While the differences in average F_{ST} values across locality type were not statistically significant, they showed a trend that supported this hypothesis. The localities on the north and south ends of SC had a lower pairwise F_{ST} value than that between PH and HW, two isolated populations that are a similar distance from one another as the north and south localities of SC (Fig. 5).

I also predicted that individuals within the same population would be more closely related to one another than to individuals in any other population (Hypothesis 2). The UPGMA

phenogram based on genetic distance (Fig. 4) indicated that overall, the results were as expected. In addition, individuals in any corridor locality were more closely related to individuals in the same corridor site than to individuals in any other site.

The way corridor localities related to one another suggested they formed one large population. Thus, I expected rural populations to have more genetic diversity than corridor populations, and in turn, for corridor populations to have more genetic diversity than isolated populations (Hypothesis 3). The average observed heterozygosity results (Fig. 5) support this hypothesis that genetic diversity was greater in rural populations than in corridor or isolated populations. However, there was no statistical difference in genetic diversity between corridor and isolated populations, indicating genetic diversity is not higher in populations connected by a corridor. In fact, the highest genetic diversity was in HW, an isolated population. This could be caused by the nearby Olmos Basin Park, which is large enough to support a big population size that could have gene flow with HW. Populations of Texas Spiny Lizards that live within the urban environment (i.e., backyards) and have gene flow with the park populations could also maintain species diversity. The lower genetic diversity found in the urban corridor and isolated populations compared to the rural population could indicate the urban environment restricts populations of Texas Spiny Lizards in a way that reduces genetic diversity. Populations may be smaller and subject to inbreeding or reduced migration from other populations caused by the difficulty of migrating through an urban environment.

The mixed results could be caused by confounding variables in the environment such as time since isolation and habitat quality. Some of the localities have been surrounded by an urban environment longer than others due to the pattern of urbanization that occurred in the history of San Antonio. Localities closer to the center of the city, such as HW, have been isolated longer.

Populations that have been isolated for longer amounts of time are more likely to be differentiated from other populations, while populations that have recently been isolated may not yet exhibit genetic differences due to inbreeding or genetic drift (Crispo & Hendry 2005). Thus, the short evolutionary timeframe that these populations have been isolated, <100 years, may not be long enough to allow the populations to show the negative effects of isolation.

There were habitat differences between the localities that could influence population dynamics for Texas Spiny Lizards. The habitat in LC had more rocks and more variation in elevation compared to SC, which was flatter and had higher vegetation coverage. The sites also vary in vegetation type, with Texas Live Oak (*Quercus fusiformis*) and Cedar Elm (*Ulmus crassifolia*) dominating HW, PH, SC, and HC, while LC was dominated by Honey Mesquite (*Prosopis glandulosa*), Ashe Juniper (*Juniperus ashei*), and Cedar Elm. These differences in habitat quality could impact the genetics of the populations. Some areas of the corridors, such as the portion of SC between McAllister Park and LBJ Park, did not contain many trees and was largely open grassland. This could cause this habitat to act as a sink instead of a corridor for this species since they are arboreal (Blair 1960, Henein & Merriam 1990).

It seems unlikely that the corridors in this study acted as sink populations. The habitat appears to be wide enough to support populations of Texas Spiny Lizards along the corridors, which may be important since they disperse short distances (Blair 1960, Simberloff 1992, Barrows et al. 2011). While this edge habitat could be low quality and act as a sink (Hobbs 1992, Lande 1998), Texas Spiny Lizards are capable of living within the urban environment when given enough trees, as they are commonly found in backyards. Gardens have been found to be important units of conservation (Goddard et al. 2010), and could affect the park populations if there is gene flow between the parks and the populations in the urban environment. This gene

flow could prevent the corridors from being sinks by widening the available habitat. Gene flow could occur through the urban environment such that it parallels the gene flow that occurs through corridors. If this is true, the urban habitat surrounding the isolated parks may be such a small barrier to dispersal that these populations are not truly isolated. When the contrast in habitat quality between the corridor and the surrounding environment is low, the value of the corridor is decreased (Rosenberg et al. 1997), which may be the case with Texas Spiny Lizards in San Antonio.

Mech and Hallet (2001) had similar results to this study, where population differentiation did not vary based on site type for deer mice. However, the deer mouse is a habitat specialist, and they found different results for the vole, a habitat specialist. For the vole, population differentiation was greatest between isolated populations, intermediate between corridor populations, and least between rural populations, which is what I expected in this study. The Texas Spiny Lizard falls between the vole and deer mouse in that it prefers certain types of habitat, but it can survive in a wide range of habitats. Thus, it is not surprising that population differentiation for Texas Spiny Lizards is not affected by site type. A habitat specialist species might be a better model organism for studying corridor effectiveness.

While most conservation studies focus on rare species, this study shows there are still benefits to studying common species. Texas Spiny Lizards provide a good model for genetic analysis of corridor effectiveness, providing large samples sizes from many populations in a range of habitats. The variation in results between this study and other previous studies raises questions about how urban corridors may influence species with different dispersal abilities, habitat preferences, or adaptabilities to living in an urban environment. The results from this study are most relevant to species with similar life history traits living in similar environments to

Texas Spiny Lizards in San Antonio, but they also provide insight to understanding all corridors. Future studies should focus on how corridors impact the population genetics of multiple species that vary in these life history traits, which will allow a more comprehensive understanding of corridor effectiveness in an urban environment. More studies, designed to test population genetics, especially in natural settings, are needed to better understand corridor effectiveness for different species (Hobbs 1992, Rosenberg et al. 1997, Gilbert-Norton et al. 2010). Combining the knowledge learned from numerous studies on different species, each facing the same type of habitat fragmentation, but responding to it differently, we can better understand what corridor qualities are most important for certain species with different life history traits. In turn, this would allow conservation efforts to target a species of concern.

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Table 1. Primer sequences, annealing temperature, and expected size for seven polymorphic microsatellite loci adapted for the Texas Spiny Lizard (*Sceloporus olivaceus*) from those adapted by Lance et al. (2009) for the Eastern Fence Lizard (*Sceloporus undulatus*). Fluorescent tags (6FAM, HEX) were placed on forward primers. The expected size (bp) is based on results from Lance et al. (2009) using *S. undulatus*. Samples that showed no PCR product after amplification with the first annealing temperature were amplified using the second annealing temperature given in parentheses.

Locus	Primer sequences (5'-3')	Annealing Temp. (°C)	Expected Size (bp)
Scun2	F: *CCCGTTGAAACACATTGGC; R: GCAGTAACACCACTAACAGGC	63	131-191
Scun3	F: #GAACACAGCCTCCCATCTCT; R: TTGCCCATCTGTTTCATCCC	63	205-275
Scun5	F: *TGCCACCCACTGAATAACCT; R: CCCATATTGTTGGAGGCAA	60 (62)	225-349
Scun6	F: #GGTCCTTTCACTTTGAGGGC; R: GCGTATTTGCATGTTTGCG	60 (62)	221-291
Scun13	F: *TGTGGGAGAAGGTCTGTTGA; R: CTGTTTGGGATGCCTGCTA	63 (58)	335-363
Scun15	F: #GCCAACAACAAACAACAGGTCT; R: TCTGCATATGGCTTCCCACA	65 (57)	353-393
Scun16	F: *ACCCTCTACACCCAGCAA; R: TCACTCCAGCCCTTTCTTCT	62 (61.6)	356-388

* 6FAM fluorescent tag, # HEX fluorescent tag

Table 2. Genetic variability of the Texas Spiny Lizard across all localities for six microsatellite loci. N is number of individuals, N_A is number of alleles, H_e is expected heterozygosity, H_o is observed heterozygosity, and *P* is probability for the Hardy-Weinberg equilibrium test.

Locus	N	N_A	H_e	H_o	*P*
Scun2	159	11	0.71	0.73	0.03
Scun3	158	19	0.91	0.68	<0.01
Scun5	157	5	0.31	0.30	0.54
Scun13	143	8	0.77	0.81	0.89
Scun15	124	6	0.56	0.48	0.68
Scun16	156	26	0.95	0.68	<0.01

Table 3. Genetic variability of the Texas Spiny Lizard at six microsatellite loci. N is number of individuals, N_A is number of alleles, H_e is expected heterozygosity, H_o is observed heterozygosity, and *P* is probability for the Hardy-Weinberg equilibrium test.

Locality	Locus	N	N_A	H_e	H_o	*P*
Headwaters	Scun2	15	5	0.67	0.93	0.18
	Scun3	15	9	0.89	0.67	0.05
	Scun5	15	3	0.30	0.27	0.14
	Scun13	14	6	0.84	0.86	0.81
	Scun15	15	5	0.45	0.53	1.00
	Scun16	15	13	0.93	0.80	0.23
Phil Hardberger	Scun2	21	7	0.70	0.86	0.81
	Scun3	20	11	0.91	0.75	0.54
	Scun5	21	3	0.38	0.38	1.00
	Scun13	18	5	0.70	0.78	0.21
	Scun15	14	2	0.07	0.07	-
	Scun16	21	16	0.90	0.57	0.00
Salado North	Scun2	22	9	0.74	0.64	0.03
	Scun3	22	9	0.86	0.55	0.01
	Scun5	20	4	0.32	0.20	0.04
	Scun13	18	7	0.75	0.78	0.96
	Scun15	16	5	0.58	0.38	0.12
	Scun16	21	16	0.91	0.71	0.00
Salado Central	Scun2	15	7	0.73	0.73	0.37
	Scun3	15	10	0.90	0.53	0.00
	Scun5	15	4	0.40	0.40	0.20
	Scun13	15	7	0.81	0.87	0.29
	Scun15	13	5	0.51	0.46	0.62
	Scun16	14	18	0.96	0.79	0.03
Salado South	Scun2	29	6	0.74	0.76	0.26
	Scun3	29	12	0.89	0.55	0.00
	Scun5	29	4	0.16	0.17	1.00
	Scun13	23	7	0.83	0.83	0.36
	Scun15	19	5	0.69	0.63	0.57
	Scun16	29	17	0.94	0.55	0.00
Leon North	Scun2	18	7	0.61	0.72	0.69
	Scun3	18	14	0.93	0.89	0.77
	Scun5	18	4	0.38	0.33	0.62
	Scun13	16	5	0.73	0.81	0.92
	Scun15	16	2	0.16	0.06	0.20
	Scun16	17	15	0.94	0.53	0.00

Table 3 Continued. Genetic variability of the Texas Spiny Lizard at six microsatellite loci. N is number of individuals, N_A is number of alleles, H_e is expected heterozygosity, H_o is observed heterozygosity, and *P* is probability for the Hardy-Weinberg equilibrium test.

Locality	Locus	N	N_A	H_e	H_o	*P*
Leon South	Scun2	19	7	0.55	0.37	0.01
	Scun3	19	11	0.86	0.68	0.12
	Scun5	19	3	0.28	0.32	1.00
	Scun13	19	7	0.80	0.89	0.73
	Scun15	19	4	0.62	0.63	0.49
	Scun16	19	16	0.94	0.79	0.24
Hays County	Scun2	20	9	0.86	0.85	0.24
	Scun3	20	11	0.91	0.85	0.22
	Scun5	20	3	0.34	0.40	1.00
	Scun13	20	5	0.57	0.70	0.74
	Scun15	20	4	0.66	0.65	1.00
	Scun16	20	12	0.90	0.80	0.05

Table 4. Pairwise F_{ST} (lower matrix) and geographic distances (km, upper matrix) between Texas Spiny Lizard localities in Bexar County and Hays County, Texas. Localities are Headwaters (HW), Phil Hardberger (PH), Salado Creek (SC) Central, North, and South, Leon Creek (LC) North and South, and Hays County (HC).

	HW	PH	SC North	SC Central	SC South	LC North	LC South	HC
HW		11.25	7.71	9.92	55.88	16.93	15.81	61.63
PH	0.033		9.86	7.22	11.50	11.48	13.79	55.50
SC North	-0.004	0.031		3.75	2.47	19.96	20.55	53.98
SC Central	-0.011	0.023	-0.006		6.15	18.33	19.75	52.02
SC South	0.026	0.059	0.014	0.006		20.71	20.75	55.88
LC North	0.007	0.009	0.006	0.002	0.029		4.70	65.28
LC South	0.015	0.052	0.010	0.016	0.023	0.015		68.87
HC	0.078	0.094	0.051	0.057	0.051	0.062	0.060	

Table 5. Genetic variability of Texas Spiny Lizards averaged across six microsatellite loci by locality. N is number of individuals, H_e is average expected heterozygosity, H_o is observed heterozygosity, and *P* is probability for the Hardy-Weinberg equilibrium test.

Locality	N	H_e	H_o	*P*
Headwaters	15	0.68	0.68	0.16
Phil Hardberger	21	0.61	0.57	<0.01
Salado North	22	0.69	0.54	<0.01
Salado Central	15	0.72	0.63	<0.01
Salado South	29	0.71	0.58	<0.01
Leon North	18	0.62	0.56	<0.01
Leon South	19	0.67	0.61	0.12
Hays County	20	0.71	0.71	0.42
Global	159	0.70	0.61	<0.01

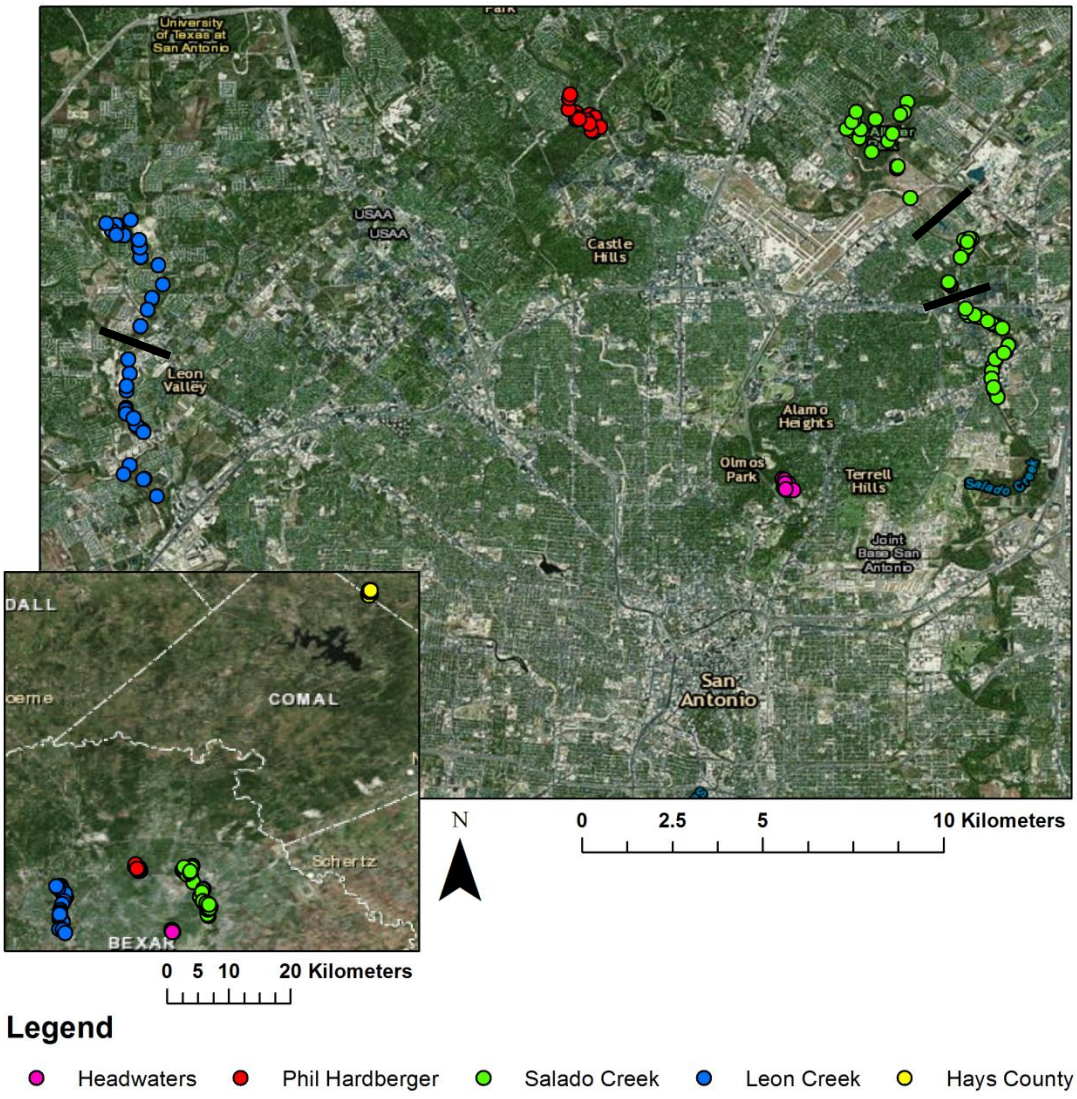

Figure 1. Map of sites in Bexar County and Hays County, Texas where 159 Texas Spiny Lizard samples were collected May through September in 2013 and 2014. Headwaters (HW) and Phil Hardberger (PH) were isolated sites, Salado Creek (SC) and Leon Creek (LC) were corridor sites, and Hays County (HC) was a rural site. Black bars indicate divisions of sites into localities.

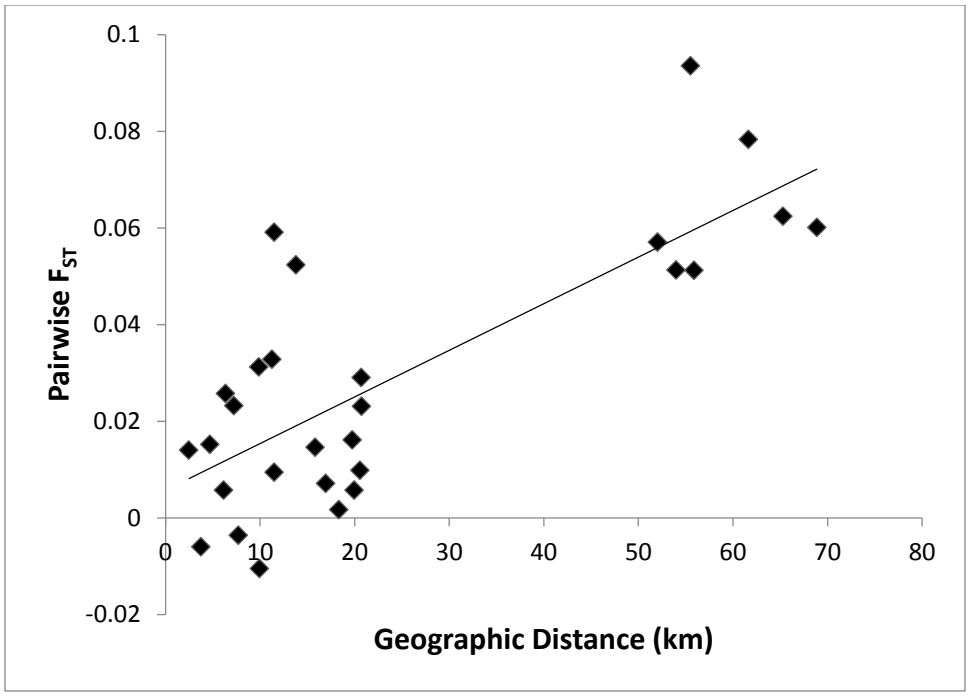

Figure 2. Geographic distance (km) versus pairwise F_{ST} for each pair of Texas Spiny Lizard localities in Bexar County and Hays County, Texas ($R^2 = 0.5868$, df = 27, $P < 0.01$).

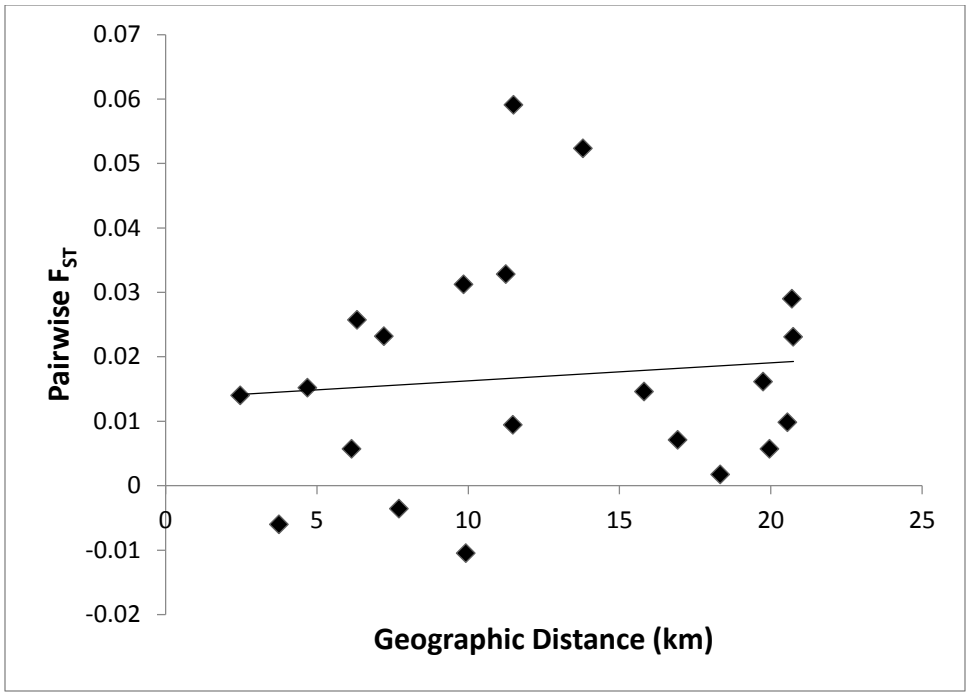

Figure 3. Geographic distance (km) versus pairwise F_{ST} for each pair of Texas Spiny Lizard localities in the urban area (i.e., excluding rural HC) of San Antonio, Texas ($R^2 = 0.0097$, df = 20, $P = 0.67$).

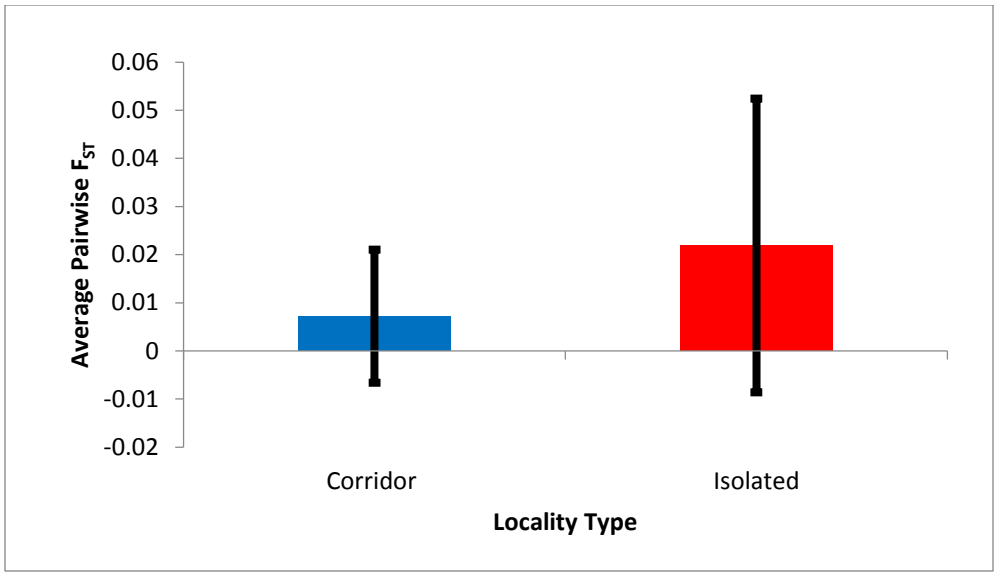

Figure 4. Average pairwise F_{ST} values for corridor and isolated Texas Spiny Lizard localities in the urban area of San Antonio. Error bars depict ±2 SE. F = 4.87, *P* = 0.110.

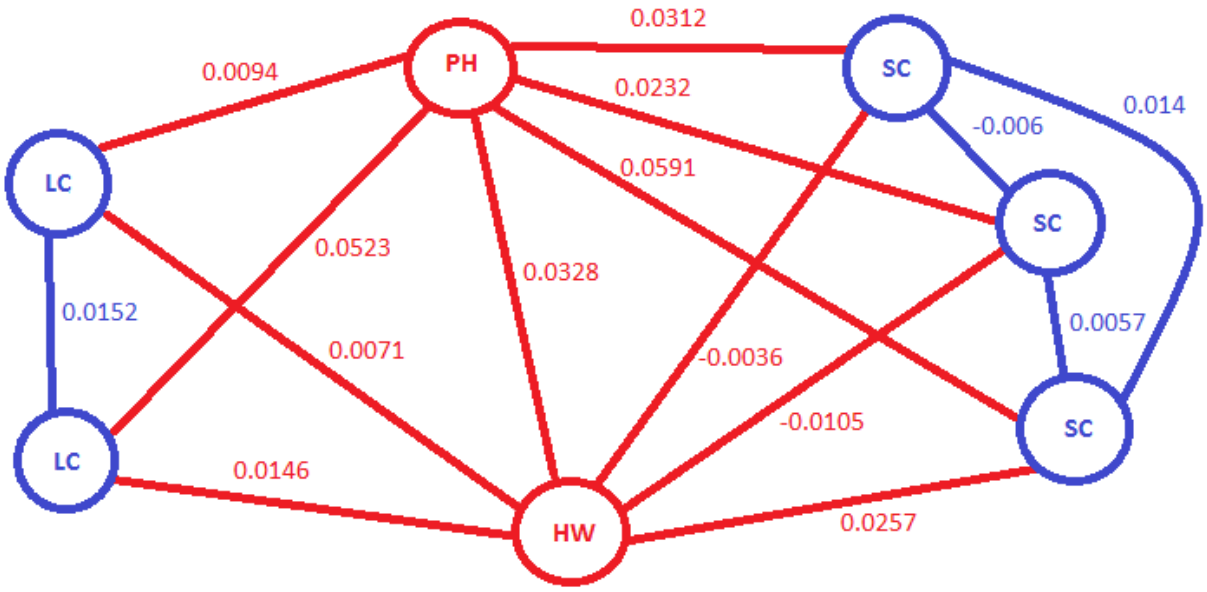

Figure 5. Diagram of urban Texas Spiny Lizard localities in San Antonio, Headwaters (HW), Phil Hardberger (PH), Leon Creek (LC), and Salado Creek (SC). Pairwise F_{ST} values are on connecting lines. Red localities and pairwise F_{ST} values are isolated. Blue localities and pairwise F_{ST} values are corridors. Geographic distances not to scale.

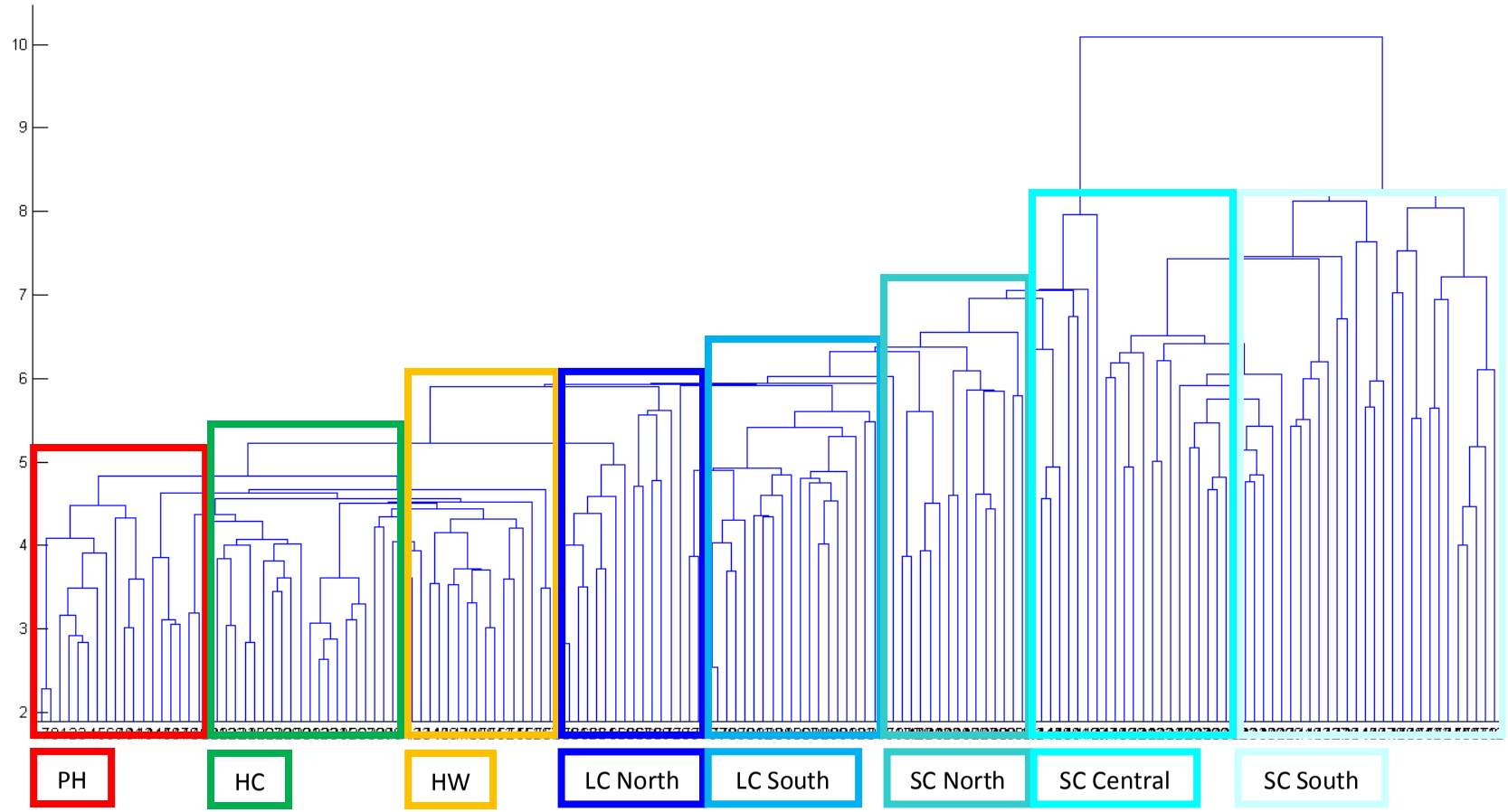

Figure 6. UPGMA phenogram of individuals constructed with MATLAB based on genetic distance calculated with GenAlEx 6.5. Boxes indicate groups of individuals that cluster closely and are within the same locality. Localities are Phil Hardberger (PH), Hays County (HC), Headwaters (HW), Leon Creek (LC), North and South, and Salado Creek (SC), North, Central, and South.

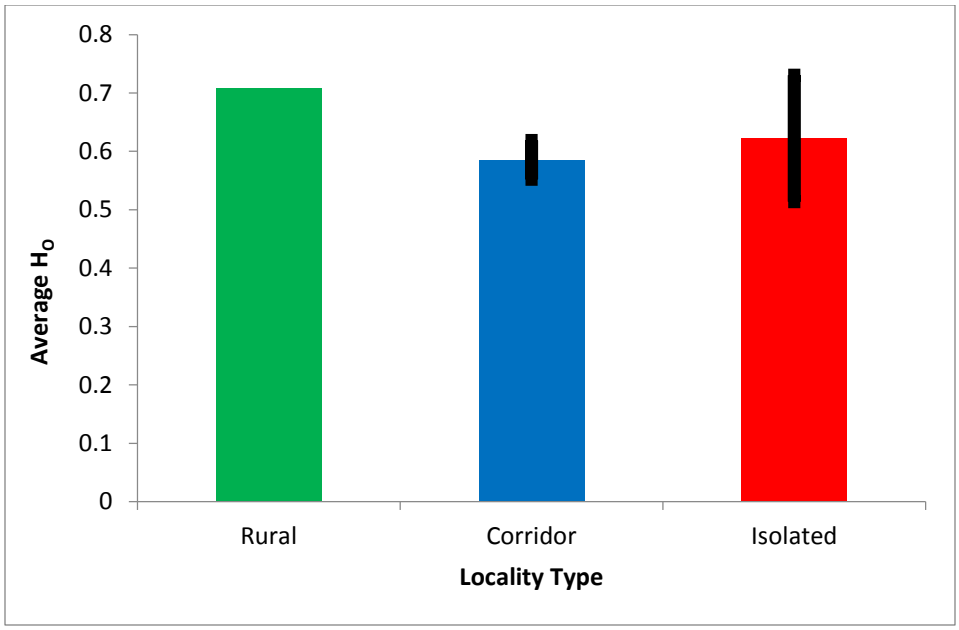

Figure 7. The average observed heterozygosity across all loci for the rural site, averaged across all corridor localities, and averaged across all isolated localities of Texas Spiny Lizards in Bexar County and Hays County, Texas. Error bars depict ±2 SE. F = 4.25, *P* = 0.108.

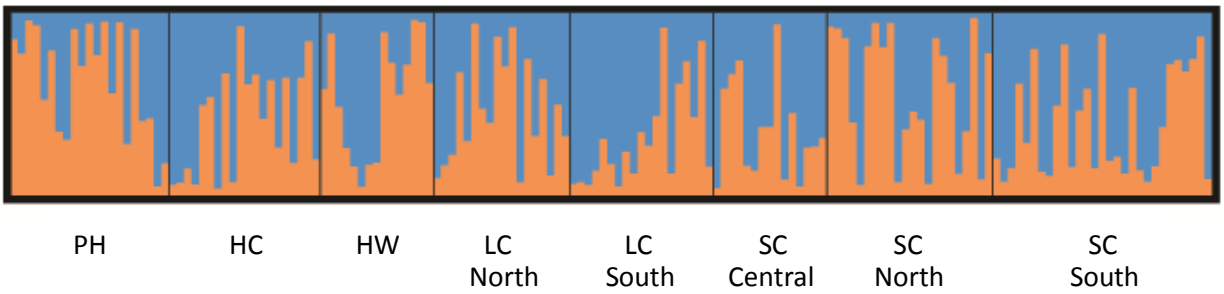

Figure 8. Cluster diagram from STRUCTURE results averaged through CLUMPP and visualized with DISTRUCT for K = 2. Each vertical bar represents an individual, and each color, blue or orange, represents a cluster. The proportion of color in each vertical bar indicates the probability that individual belongs to that colored cluster. Texas Spiny Lizard localities are Phil Hardberger (PH), Hays County (HC), Headwaters (HW), Leon Creek (LC) North and South, and Salado Creek (SC) Central, North, and South.

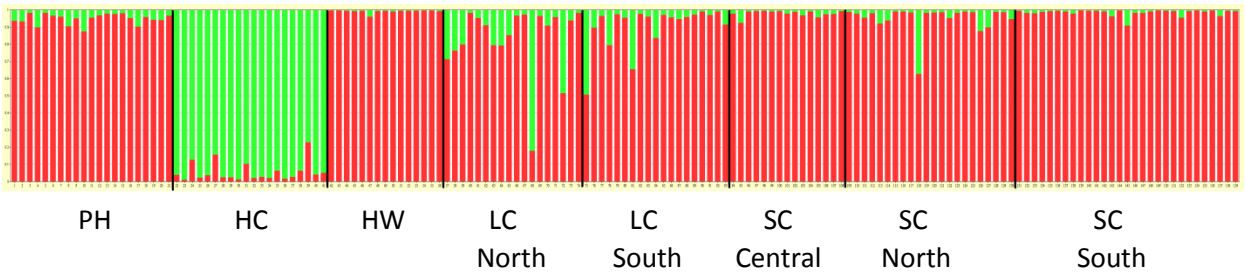

Figure 9. Cluster diagram for K = 2 from TESS analysis. Each vertical bar represents an individual, and each color, red or green, represents a cluster. The proportion of color in each vertical bar indicates the probability that individual belongs to that colored cluster. Texas Spiny Lizard localities are Phil Hardberger (PH), Hays County (HC), Headwaters (HW), Leon Creek (LC) North and South, and Salado Creek (SC) Central, North, and South.

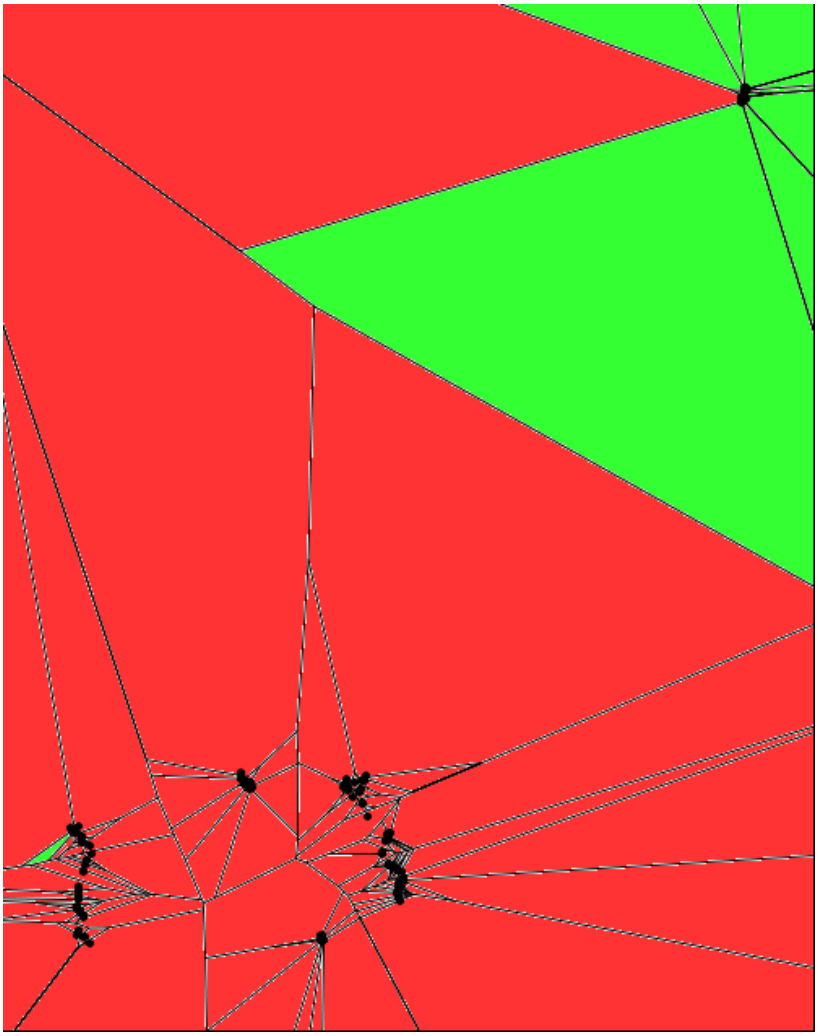

Figure 10. Geographic tessellation cluster diagram for K = 2 from TESS analysis. Black points indicate Texas Spiny Lizard sample locations in Bexar County and Hays County, Texas. Each color, red or green, represents a cluster.