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RESEARCH ARTICLE

The scale of genetic differentiation in the Dunes Sagebrush-Lizard (*Sceloporus arenicolus*), an endemic habitat specialist

Lauren M. Chan · Lee A. Fitzgerald · Kelly R. Zamudio

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Abstract The Dunes Sagebrush-Lizard (*Sceloporus arenicolus*) is a North American species endemic to sand-shinnery oak habitats of the Mescalero and Monahans sand dunes in eastern New Mexico and western Texas. This lizard is listed as Endangered in New Mexico and exhibits habitat specificity at several geographic scales. Dunes Sagebrush-Lizards are only found in topographically complex shinnery oak (*Quercus havardii*) dominated landscapes within their small geographic distribution and are not found in surrounding human-altered landscapes. Within suitable sand-shinnery oak habitat, individuals predominantly occupy non-vegetated sand dune blowouts and utilize blowouts with particular physical characteristics due to thermoregulatory, reproduction, and foraging requirements. Here, we examined historical and contemporary patterns of genetic differentiation with respect to the current distribution of suitable habitat at multiple spatial scales using mitochondrial DNA sequences and microsatellite data from individuals throughout the entire range. We found three genetic clusters of individuals generally concordant with geographic regions and low sequence divergence at mitochondrial loci suggesting a recent origin of these populations. We also found high levels of genetic structure at microsatellite loci among populations within each of these groups indicating restricted gene flow at intermediate scales. Despite high habitat specificity, we did not detect genetic structure among sand blowouts at finer spatial scales. Within each population, matrices comprised of both sand blowouts and vegetated shinnery oak patches are necessary for genetic connectivity, but the fine scale spatial arrangement of blowouts may not be as critical. We discuss our results with respect to the scale of landscape heterogeneity and habitat connectivity and consider the conservation implications for this threatened taxon.

Keywords Mescalero sands · Population genetics · Sand-shinnery oak · Phylogeography · Habitat alteration

L. M. Chan · K. R. Zamudio
Department of Ecology and Evolutionary Biology, Cornell University, Corson Hall, Ithaca, NY 14853-2701, USA

L. M. Chan (✉)
Department of Integrative Biology, 401 WIDB, Brigham Young University, Provo, UT 84602, USA
e-mail: laurenchan1@gmail.com

L. A. Fitzgerald
Section of Ecology and Evolutionary Biology, Department of Wildlife and Fisheries Sciences, Texas A & M University, College Station, TX 77843-2258, USA

Introduction

Specialists are often dependent on resources or environmental conditions that are rare or patchily distributed, thereby increasing the likelihood of differentiation within species due to reduced genetic diversity or local extinction within patches (Harrison and Hastings 1996; Hanski 1999; Hokit and Branch 2003a) and limited gene flow among patches (Kelley et al. 2000; Brouat et al. 2003; Hoehn et al. 2007). Indeed, empirical studies show that specialist taxa have higher levels of genetic structure at similar spatial scales than closely related, co-occurring generalists (e.g. Kelley et al. 2000; Brouat et al. 2003; Zayed et al. 2005; Hoehn et al. 2007). The size and distribution of suitable habitat patches, the nature of the surrounding matrix, and the vagility of the organism directly affects the degree of spatial connectivity (Arnaud 2003; Funk et al. 2005; Spear et al. 2005). Genetic structure also reflects evolutionary history, thus, recognizing the roles of both

historical and contemporary processes can elucidate the role of specialization to patterns of genetic differentiation. By identifying the scale of historical and current limits to gene flow, we can better understand how patch size, patch connectivity, and landscape characteristics affect population persistence and the maintenance of genetic diversity (Wiens 2001; Manel et al. 2003).

We examined the evolutionary history and contemporary population genetic structure of the Dunes Sagebrush-Lizard (*Sceloporus arenicolus*) to determine the importance of habitat heterogeneity and landscape features to the persistence of this endemic habitat specialist. *Sceloporus arenicolus* is found exclusively within the sand-shinnery oak habitat of the Mescalero and Monahans sand dune regions of eastern New Mexico and western Texas (Degenhardt et al. 1996). This lizard's distribution includes a large sickle-shaped region running north and south along the base of a caprock plateau with three smaller and potentially isolated regions to the north (based on surveys by Fitzgerald et al. 1997). Individuals are patchily distributed within this range due to habitat heterogeneity and specialization, therefore, attributes of the landscape at particular spatial scales may be critical to the maintenance of connectivity among populations. At the range-wide scale, grassland, mesquite scrub and human-altered landscapes fragment regions of sand-shinnery oak habitat. Within areas of contiguous sand-shinnery oak habitat, populations are found only in areas of topographic complexity with a mosaic of open sandy depressions (referred to as blowouts) and vegetated patches of sand-shinnery oak (*Quercus havardii*) scrub. At finer-scales individuals are found almost exclusively within blowouts, but are not uniformly distributed among them; *S. arenicolus* prefers large blowouts with specific topographic, thermal, and physical characteristics (Sena 1985; Fitzgerald et al. 1997). Thus, they do not occupy all blowouts and are additionally absent from many seemingly suitable sites possibly due to local extinction or isolation (Fitzgerald et al. 1997).

Sceloporus arenicolus is listed as Endangered by the New Mexico Department of Game and Fish and is a candidate for federal listing by the US Fish and Wildlife Service (Federal Register September 12, 2006). Habitat destruction from the application of herbicide to remove shinnery oak and fragmentation due to oil and gas development pose threats to Dunes Sagebrush-Lizard populations (Snell et al. 1997). Because of this lizard's dependence on already patchily distributed sand dune blowouts, anthropogenic alterations to the habitat are likely to lead to increased disruption of movement and patch connectivity. Understanding evolutionary patterns of population differentiation and identifying the spatial scale and landscape features that permit continued genetic connectivity are important for effective conservation actions.

Using mitochondrial DNA (mtDNA) sequences and multilocus microsatellite genotypes, we examined the geographic distribution of genetic variation across the entire range of this endemic species and interpreted our results in light of the features of the Mescalero and Monahans sand dune landscapes. We expected that specialization to the sand-shinnery oak habitat would result in a genetic signature of reduced population size (i.e. bottleneck) associated with colonization followed by demographic expansion in the novel habitat. In addition we predicted that limited gene flow would be reflected in genetic differentiation at microsatellite loci and indicate the importance of current landscape features to genetic connectivity. Thus, our goals were to: (1) determine how both historical processes and contemporary landscape characteristics have influenced differentiation in this habitat specialist, (2) identify the geographic scale of genetic differentiation, and (3) consider the potential consequences of anthropogenic alterations to the landscape for the persistence of *S. arenicolus*.

Methods

Population sampling and laboratory protocols

We obtained tissues samples from throughout the range of *S. arenicolus* from ethanol-preserved specimens in the Museum of Southwestern Biology (MSB) and individuals captured during the field seasons of 2003–2006. We also included as outgroups two samples of *Sceloporus graciosus* from the *graciosus* clade sister to *S. arenicolus* (Wiens and Reeder 1997; Frabotta 2002) collected from northwestern New Mexico. Tissues from live-caught individuals were sampled as toe and tail clips preserved in 100% EtOH; sampled individuals were released at the point of capture. We isolated DNA from tissues with either the QIAquick DNAeasy Extraction Kit following manufacturers protocols or by Chelex extraction. Chelex extractions consisted of tissue incubation in 150 µl of a 5% Chelex solution (Chelex-100; BioRad) with 19 µg proteinase K for 180 min at 55°C and 10 min at 99°C.

We sequenced two mtDNA gene regions for 54 individuals of *S. arenicolus* from throughout their entire range and two *S. graciosus* from northwestern New Mexico (Fig. 1). Amplifications via the polymerase chain reaction (PCR) were conducted at a total volume of 25 µl and consisted of 1 µl DNA template, 1% Hi-Di formamide, 1× *Taq* buffer, 1.5 mM $MgCl_2$, 1.9 µM dNTPs, 1.5 µM of each primer (forward and reverse), and 0.625 U *Taq* polymerase. We targeted a portion of the cytochrome-*b* gene (cyt-*b*) with the primers MVZ05 and MVZ16 (Smith and Patton 1991; da Silva and Patton 1993) and the entire NADH dehydrogenase

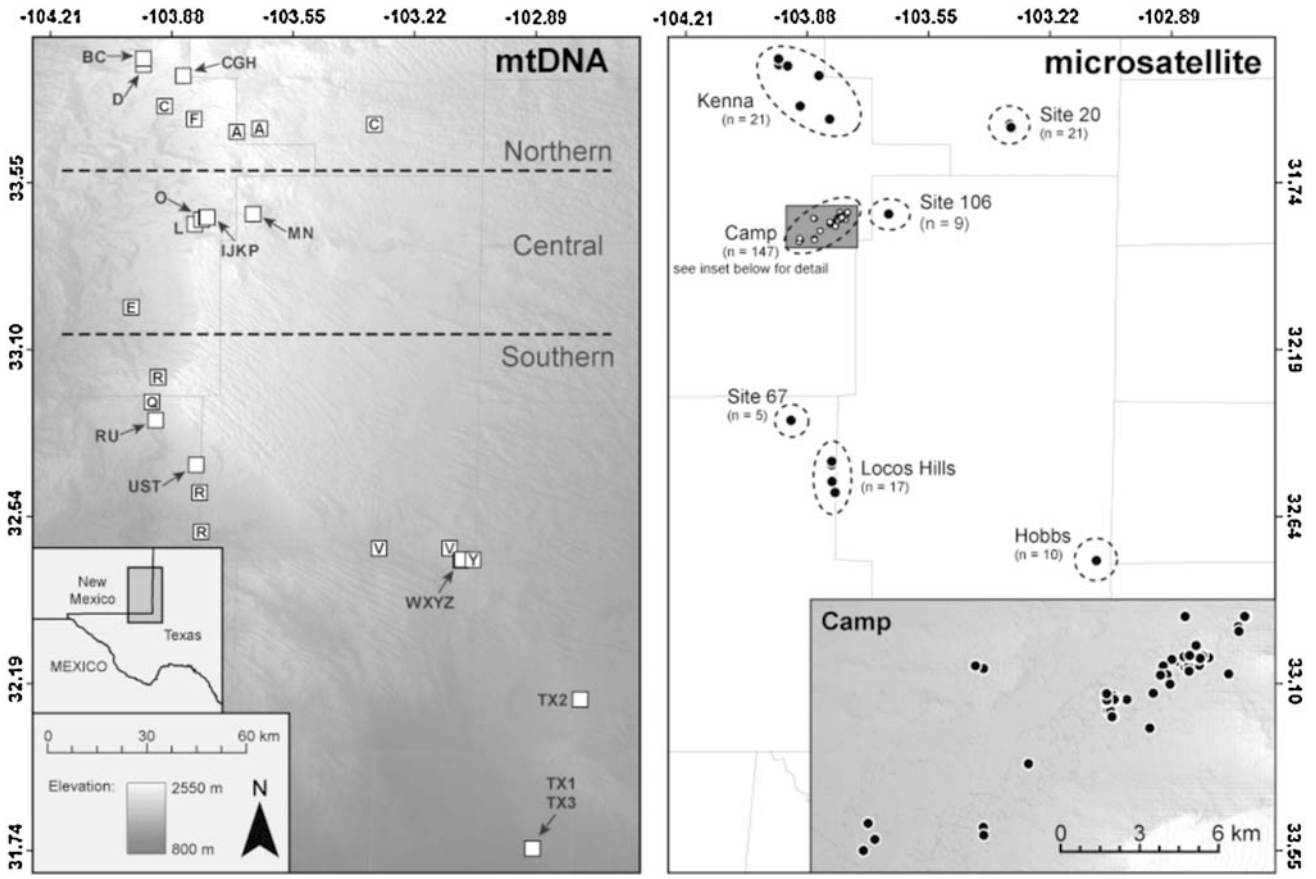

Fig. 1 Collection localities for *S. arenicolus* included in the mitochondrial (left) and microsatellite datasets (right). Mitochondrial haplotypes corresponding to Fig. 3 are indicated by letters on the elevation-shaded map. The seven groupings used for population-based analyses of microsatellite data are delineated with dashed lines with sample sizes are in parentheses. Inset shows the extent of fine-scale sampling for the Camp population

subunit 1 (ND1), flanking tRNAs (Leu and Ile), and 16s ribosomal RNA (16S) with the primers tMet and 16dR (Leaché and Reeder 2002). PCR profiles consisted of an initial denaturation for 5 min at 94°C, 35 cycles of 30 s at 94°C, 30 s at 45°C or 54°C (cyt-*b* and ND1, respectively), and 1 min at 72°C, followed by a final 15 min extension at 72°C. PCR products were incubated with Exonuclease I (10 units) and SAP (1 unit) to remove unincorporated nucleotides/primers and cycle sequenced in both directions using Big Dye termination sequencing chemistry and the primers used in initial amplifications. Sequencing reactions were done in a total volume of 5 µl with 1 µl cleaned PCR product, 0.24 µM primer, 1 µl Ready Reaction Mix, and 0.5 µl Sequencing Buffer (Applied Biosystems). Cycle sequencing products were purified with Sephadex G-50 and visualized on ABI 3100 and ABI 3730 automated sequencers. Electropherograms were checked by eye prior to constructing contigs for each gene region for each individual in the program Sequencher v4.5 (GeneCode).

To investigate contemporary genetic structure at finer geographic scales, we genotyped 230 individuals from seven sampling localities throughout the range of *S. arenicolus* (Fig. 1). These populations were delineated based on the geographic proximity of individual collection localities and habitat continuity. We genotyped individuals at seven polymorphic microsatellite loci using primers and amplification conditions described in Chan et al. (2007). Because our microsatellite dataset focused primarily on seven discrete sampling localities, this dataset included some, but not all individuals included in the mtDNA dataset. Amplicons were electrophoresed on an ABI 3100 Automated Capillary DNA Sequencer and genotypes were sized by comparison with GeneScan-500 LIZ size standard using the software Genemapper v3.5 (Applied Biosystems).

MtDNA data and phylogenetic history

We aligned sequences to the mtDNA genome of *S. occidentalis* (GenBank AB079242) in MacClade v4.08 (Maddison and Maddison 2003) to verify gene regions and check for stop codons and nonsense mutations. Alignments were straightforward with a single base pair insertion–deletion occurring between outgroup and ingroup haplotypes in tRNA-Ile. We created separate alignments for the

cytochrome-*b* (cyt-*b*) fragment and the ND1 plus flanking regions sequence (ND1-tRNAs-16S) as well as a concatenated alignment including both gene regions. We identified identical combined sequences and eliminated redundant haplotypes from the final mtDNA dataset using Collapse v1.2 (Posada 2004). Unique haplotypes for each gene region were deposited in GenBank (EF558623–EF558664).

We inferred evolutionary relationships among *S. arenicolus* mitochondrial haplotypes using parsimony networks, Bayesian inference (BI), and topology tests in a maximum likelihood (ML) framework. We constructed haplotype networks in TCS 1.21 (Clement et al. 2000) using a 95% parsimony connection threshold disregarding ambiguities between sequences. For Bayesian phylogenetic inference, we first used MrModeltest (Nylander 2004) and the Akaike Information Criterion (AIC) to infer the models of sequence evolution that best fit each partition of our dataset: we estimated models separately for first, second, and third codon positions of cyt-*b* and ND1, and non-coding regions). We conducted partitioned Bayesian analyses in MrBayes 3.1.2 (Ronquist and Huelsenbeck 2003). We applied the F81 model to the second-position cyt-*b* partition and the GTR model to third-position ND1 partition; all other data partitions followed the K80 model of sequence evolution. The prior state frequencies were set as flat Dirichlet distributions for all partitions except for first-position cyt-*b* which was set as equal. MrBayes analyses consisted of two runs each of four chains sampling every 1,000 generations for 10,000,000 generations. We verified convergence by examining the trends in natural log likelihood scores for all parameters and disregarded the initial 1,001 trees from each run as burn-in. We estimated the 50% majority-rule consensus topology with branch-lengths and posterior probabilities for each node in MrBayes.

To test the robustness of inferred haplotype clades, we used ML parametric bootstrap topology tests. We determined the model of sequence evolution that best fit our combined sequence data by the AIC using Modeltest (Posada and Crandall 1998). Unconstrained ML topology searches for the combined mitochondrial dataset were implemented in PAUP* 4.0b10 (Swofford 2002) using the preferred model, a general-time-reversible model of sequence evolution with six substitution rates, a proportion of sites invariable, and equal rates among variable sites (GTR + I). We rooted topology searches with *S. graciosus* as the sister clade to all *S. arenicolus* and conducted 100 heuristic search replicates. Starting trees were obtained by random stepwise addition sequence and we used the TBR branch-swapping algorithm. We tested three alternative hypotheses regarding the monophyly of haplotypes from each of three geographic regions (Table 1). For each alternative hypothesis, we estimated the most likely topology and branch lengths for the mtDNA dataset using 100 heuristic search replicates constrained to the particular skeletal constrained topology. We then used Mesquite 1.1 (Maddison and Maddison 2006) to generate 200 random DNA sequence datasets of 1,759 base pairs simulated on the preferred tree from the constrained search using the same model of nucleotide evolution assumed for phylogenetic inference. For each of the randomized datasets, we conducted one constrained and one unconstrained analysis of 100 heuristic search replicates. We used the differences in the tree scores from the two analyses of each dataset to construct the null distribution for comparison with our empirical data; the significance of the test statistic was estimated using a one-sided *t*-test (Goldman 1993).

Table 1 Topologies and tree scores for unconstrained and constrained topologies used for parametric bootstrap tests of alternative topologies

Topology	Score
Unconstrained	3062.9724
(Northern) (Central + Southern)	3066.4058
((Northern + Central) Southern)	3065.3907
(Northern (Central + Southern))	3062.9724

Tests did not reject any of these constrained topologies

Microsatellite data and population level genetic structure

We used the program HP-Rare (Kalinowski 2004) to estimate overall and private allelic richness at each locus correcting for variation in sample size by standardizing counts for a population size of five individuals. Because extremely uneven sampling can lead to erroneous estimates of allelic richness and private allelic richness even after correction, we omitted the Camp locality ($n = 147$) from these calculations. For all populations, we tested multilocus genotypes for departure from Hardy–Weinberg equilibrium (HWE) and evidence of linkage disequilibrium using randomization tests in Genepop v3.4 (Raymond and Rousset 1995). A Markov chain method was used (Guo and Thompson 1992) with 5,000 dememorization steps and 1,000 batches of 10,000 iterations each to determine significance for global and within population comparisons.

We used distance and model-based approaches to infer population structure, connectivity, and admixture from our microsatellite data set. First, we calculated pairwise F_{ST} (Weir and Cockerham 1984) among the seven sampling localities in Fstat v2.9.3 (Goudet 1995) and used permutation tests with 10,000 replicates to determine levels of significance after Bonferroni adjustment for multiple comparisons. To insure that our a priori population designations were not obscuring patterns of differentiation, we also examined population structure using Bayesian assignment

tests. Bayesian approaches to estimate population differentiation do not require assumptions about the source of sampled individuals. We conducted Bayesian assignment tests using Markov chain Monte Carlo (MCMC) sampling methods implemented in Structure v1.2 (Pritchard et al. 2000; Falush et al. 2003) to infer the number of genetic clusters (K) and identify genetic discontinuities among sampled individuals. For each K from $K = 1$ to 13, we conducted ten independent MCMC runs of 1,000,000 steps following a 250,000 step burn-in. For each run we assumed no correlation of allele frequencies among populations, did not use information on population of origin, and followed an admixture model with a single value of lambda inferred for all populations. We examined the rate of change in the mean and variance in log likelihood scores between successively increasing values of K to identify the most probable number of clusters as suggested by Evanno et al. (2005). For the most probable K, we examined individual membership coefficients (q) and the associated 90% probability intervals for assignment to each of the K clusters. Values of q less than 0.90 had wide 90% probability intervals, thus, we chose $q = 0.90$ as a cutoff for admixed individuals. For each population, we calculated the proportion of individuals that showed evidence of admixture (all values of $q \leq 0.90$). We used Distruct (Rosenberg 2004) to plot the membership coefficients, q, of individuals to each of the K clusters with individuals ordered geographically from the northeastern to the southeastern parts of the range.

To determine whether individuals exhibited non-random genetic similarity at fine spatial scales, we conducted spatial autocorrelation analyses implemented in GenAlEx 6 (Peakall and Smouse 2006). Our most extensive spatial sampling was for the Camp locality, thus we used these 147 individuals and calculated indices of spatial autocorrelation (r_C) at 1 km distance class intervals and used 999 bootstrap replicates to estimate 95% confidence intervals. We conducted 999 permutations of individuals across distance classes to determine whether r_C was significantly different from zero at each distance class from 1 to 16 km (Smouse and Peakall 1999).

Historical demographics

To test for population expansion in geographic regions, we calculated F_S (Fu 1997) in Arlequin v3.1 using 10,000 randomizations of the data to determine the significance of the test statistics. F_S calculates the probability of k or more alleles given the average number of pairwise differences individuals (Fu 1997) and is particularly sensitive to population expansion and more powerful than other moment estimators (Ramos-Onsins and Rozas 2002).

We also estimated historical demographic parameters assuming a model of isolation with migration in the program IM (Nielsen and Wakeley 2001; Hey and Nielsen 2004) for our mtDNA dataset. IM uses a Bayesian coalescent framework to estimate demographic parameters for a pair of populations. We divided samples into Northern, Central, and Southern geographic groups based on phylogenetic relationships and sampling locality (Fig. 1). For two pairs (Northern–Central, and Central–Southern) we estimated time since divergence ($t = t\mu$), the effective size of each population ($\theta_1 = 4N_1\mu$ and $\theta_2 = 4N_2\mu$), the ancestral effective size ($\theta_A = 4N_A\mu$), and the migration rate between populations ($m_1 = m_1/\mu$ and $m_2 = m_2/\mu$). We performed initial searches varying MCMC search parameters to assure adequate mixing and convergence. Final runs for the mtDNA data set consisted of ten chains heated linearly, an initial burn in of 250,000 steps, and sampling every ten steps for over 20,000,000 generations. We compared the posterior probability densities for t from each run to determine the order of divergence among these three groups and examined the posterior probabilities for evidence of unequal effective sizes ($\theta_1 > \theta_2$), population expansion ($\theta_1 > \theta_A$; $\theta_2 > \theta_A$), and asymmetrical migration ($m_1 > m_2$).

Results

Molecular data

We collected a total of 1,759 base pairs (bp) of mtDNA sequence data for *S. arenicolus* and *S. graciosus*. The mitochondrial dataset corresponds to partial cyt-*b* (608 bp) sequence, complete sequences of ND1 (969 bp) and tRNA-Leu (75 bp), and fragments of 16S (29 bp) and tRNA-Ile (68 bp). We found 31 unique haplotypes (29 for *S. arenicolus* and two for *S. graciosus*), seven of which differed from other haplotypes only by ambiguous base calls. *Sceloporus arenicolus* haplotypes contained 33 variable sites.

The diversity of mitochondrial haplotypes within an area differed across the range. Among northern localities we found six unique haplotypes represented in 17 individuals sampled with only a single haplotype among the four individuals from the easternmost collection locality. Haplotypes of the three individuals from the easternmost central locality differed only by an ambiguous base. Among the seven individuals from the remaining central localities, we detected four haplotypes. A single haplotype was found in nine of the 14 individuals from the westernmost southern collection localities and we recovered five haplotypes among the nine individuals in the southeasternmost New Mexico localities. The three individuals from Texas had unique and distant haplotypes (Figs. 2, 3).

Allelic diversity at seven microsatellite loci varied from 5 to 24 alleles per locus (average = 15.1). Mean population specific allelic richness for the six smaller sampling

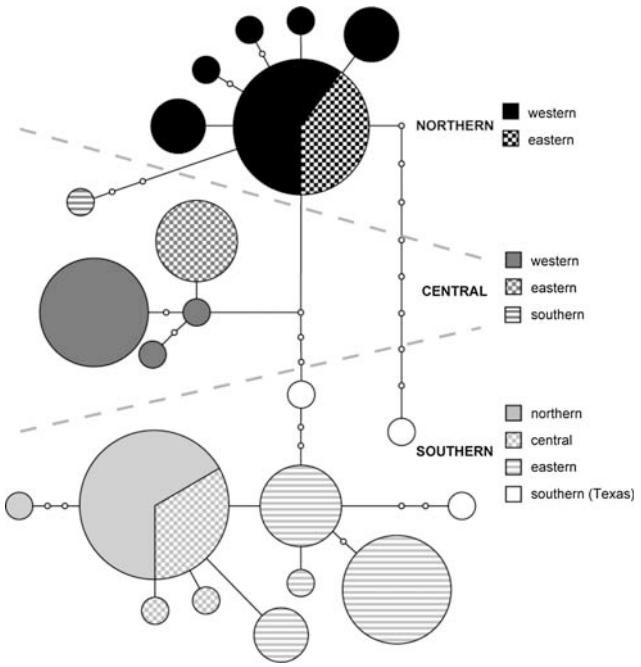

Fig. 2 Haplotype network based on 1,759 base pairs of mtDNA sequence of *S. arenicolus*. Shared haplotypes are indicated by circles with their area proportional to the number of sampled individuals with that haplotype. Unsampled haplotypes are represented by small open circles. Shade and pattern correspond to general collection locality of individuals

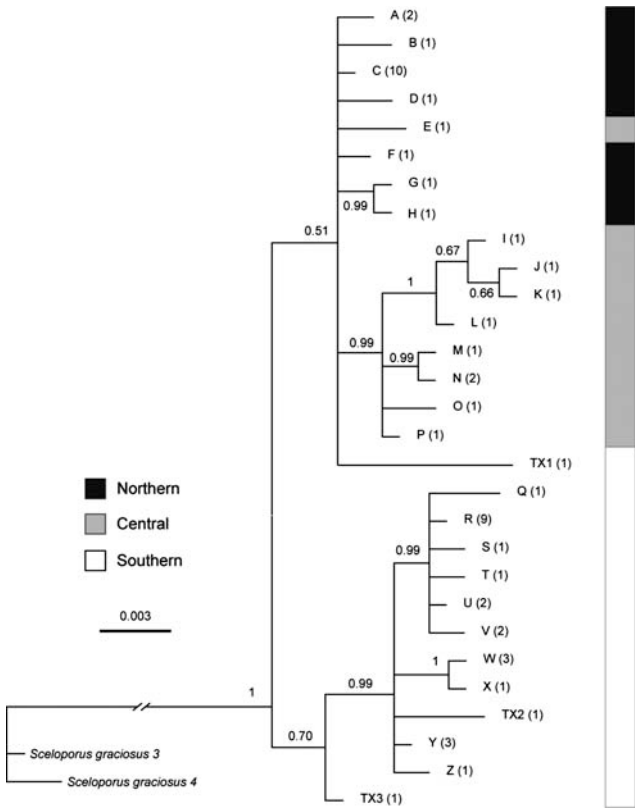

Fig. 3 A 50% majority-rule consensus phylogeny from partitioned Bayesian analysis of mtDNA sequences. Posterior probabilities are indicated at the nodes and branch lengths reflect the expected number of substitutions per site. Haplotype letters at the tips with the number of individuals with that haplotype in parentheses correspond to Fig. 1

localities adjusting for differences in sample sizes ranged from 2.98 to 4.20 alleles/locus (Fig. 4). The average number of private alleles per locus across these six populations after rarefaction ranged from 0.17 at Site 67 to 0.83 at Kenna. Expected heterozygosity within populations ranged from 0.520 at Site 20 to 0.746 at Site 67 and was 0.792 at Camp. We found no evidence for departure from HWE at any locus in any of the seven localities at $\alpha = 0.05$ after Bonferroni correction for multiple comparison. We also did not detect significant linkage disequilibrium for any locus pairs within or among populations (all $P > 0.177$).

Phylogenetic history

Mitochondrial haplotypes differed by one to nine mutational steps with an average of 1.86 steps (Fig. 2). Haplotype networks recovered three distinct groups generally concordant with geographic locality. One haplotype from the southern portion of the central region, and one haplotype from Texas, were more closely related to the most common haplotype found in the northern region. The other two Texas samples were associated with southern region haplotypes.

The monophyly of all *Sceloporus arenicolus* with respect to the two sampled *S. graciosus* was strongly supported in Bayesian inference (Fig. 3). We found strong nodal support for the monophyly of central and southern

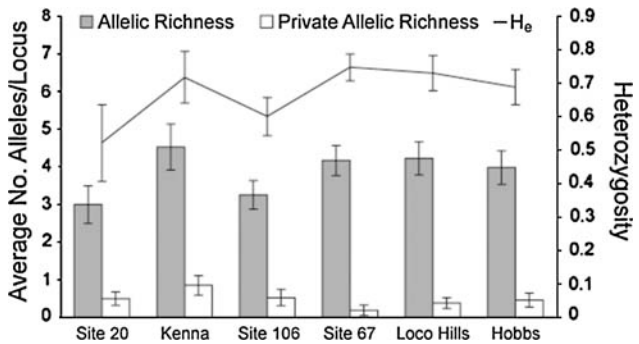

Fig. 4 Average allelic richness (gray bars) and private allelic richness (white bars) corrected for sample size and expected heterozygosity (line graph) with standard error bars for six genotyped populations (Camp is omitted)

haplotype groups recovered in parsimony networks (Posterior Probabilites, PP, = 0.99 and 0.99), though support for one Texas sample as sister to the remaining southern samples was weaker (PP = 0.70). Support for the relationships among these geographic areas were weak. Our inferred phylogenies using BI found that northern haplotypes, plus one central and one southern haplotype, formed

a basal polytomy relative to the remaining haplotypes sampled. We were unable to reject our alternative hypotheses in topology tests constraining individuals based on geographic locality (Table 1). Support for the three constrained topologies were equally probable compared to the most well-supported topology from ML methods. Therefore, we found strong support for three distinct clades, but no resolution of the relationships among them.

Population level genetic structure

Pairwise estimates of F_{ST} based on microsatellite data for the seven collection localities revealed significant differentiation among all but one population pair with significant F_{ST} values ranging from 0.0572 to 0.3471. In general, pairwise values of F_{ST} were greater between populations from different mitochondrial haplotype clades and geographic regions (Table 2). The average F_{ST} within regions was 0.1000 (range: 0.0752 to 0.1169) whereas the average F_{ST} for pairwise comparisons of populations in different regions was 0.1969 (range: 0.0572 to 0.3471).

Using the method by Evanno et al. (2005), we found support for three clusters in Bayesian assignment tests based on microsatellite data, corroborating the results from mtDNA (Fig. 5). The degree to which individuals showed shared history with multiple regions varied across populations and likely reflects evidence of recent gene flow. All 21 genotyped individuals from Site 20 belonged unambiguously to the northern cluster. Only eight of 21 individuals from Kenna were unambiguously assigned to this cluster whereas the remaining individuals were assigned to both northern and central clusters, or to all three clusters (Fig. 5). All individuals from Site 106 and most individuals from Camp were assigned with high probability ($q > 0.9$) to a central cluster. The other individuals from Camp showed evidence of past gene flow ($q_{max} < 0.9$) with northern and/or southern clusters (Fig. 5). All southern individuals, with the exception of one collected from Hobbs fell exclusively within the southern cluster.

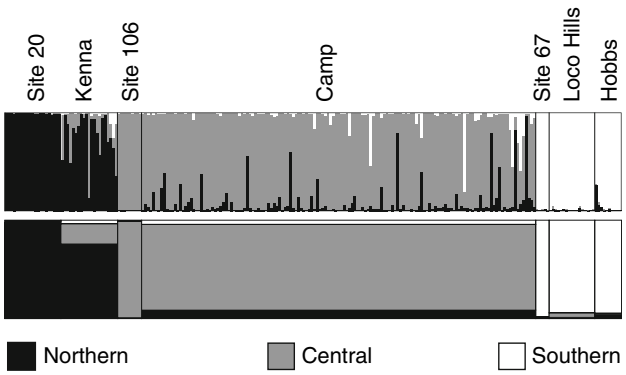

Fig. 5 Genetic membership for all genotyped *S. arenicolus* inferred from Bayesian assignment tests in Structure. Membership to each of three regions are plotted for each individual (top) and as a population average (bottom)

We did not find significant spatial autocorrelation at fine spatial scales. Estimates of spatial autocorrelation, r_C, ranged from −0.038 to 0.034 across distance classes but were not significantly different from zero or permuted values.

Historical and contemporary demographics

Our estimates of F_S did not support population expansion in the central or southern regions (central: $F_S = 0.271$, $P = 0.558$; southern: $F_S = -2.676$, $P = 0.097$), but did show weak evidence of population expansion in the northern region ($F_S = -2.467$, $P = 0.022$) according to the $P < 0.02$ criteria for significance at $\alpha = 0.05$ (see Fu 1997).

For each dataset, Bayesian estimates of historical demographic parameters under the isolation with migration model in IM converged on the same posterior distributions over multiple runs. Current population sizes (θ_1 and θ_2)

Table 2 Pairwise F_{ST} estimates based on genotyped individuals from seven collection localities

		Site 20	Kenna	Site 106	Camp	Site 067	Loco Hills	Hobbs
Northern	Site 20	-						
	Kenna	0.116 ***	-					
Central	Site 106	0.347 ***	0.191 ***	-				
	Camp	0.183 ***	0.057 ***	0.092 ***	-			
Southern	Site 067	0.313 **	0.162 ***	0.251 *	0.141 ***	-		
	Loco Hills	0.250 ***	0.115 ***	0.253 ***	0.131 ***	0.046	-	
	Hobbs	0.255 ***	0.113 ***	0.258 ***	0.130 ***	0.117 **	0.075 ***	-

Gray boxes unite populations within the same geographic region. *$P \leq 0.05$, **$P \leq 0.01$, ***$P \leq 0.001$

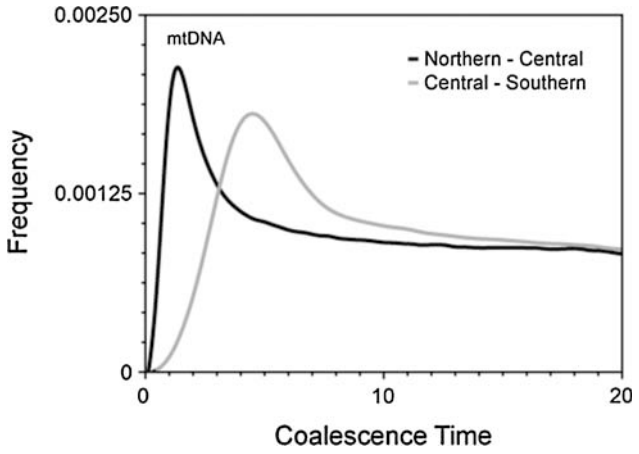

Fig. 6 Posterior probability densities for coalescence time, *t*, of mtDNA under an isolation-by-migration model implemented in IM

were not significantly different from one another or from inferred ancestral populations sizes for either population pair. Migration estimates were low (0.005) for all populations, however, the posterior probability for greater θ scaled migration into the central region from the northern region was 0.710 weakly suggesting the possibility of asymmetry in migration between these regions. We did not find any support for asymmetrical migration between central and southern regions. The posterior probability distributions for divergence time, *t*, had long, non-zero, right handed tails for both datasets, however, the peak divergence time between the northern and central regions was less than that between the central and southern region (Fig. 6).

Garza and Williamson (2001) compared measures of *M* in taxa with stable demographic histories and those with recent population reductions. In their review, *M* was greater than 0.82 in stable populations and less than 0.70 for populations with known reductions in size. Our seven populations showed *M* between 0.567 and 0.884 with a mean of 0.682. Three populations (Site 106, Site 67, and Hobbs) showed evidence of population reduction and Camp showed evidence of population stability. The remaining populations (Site 20, Kenna, and Loco Hills) had *M* between 0.70 and 0.82, and thus, we could not infer the demographic histories of these three sites.

Discussion

We detected genetic differentiation among *S. arenicolus* populations at several spatial scales throughout its limited range that likely reflect historical patterns of diversification as well as currently restricted gene flow imposed by specialization to sand dune blowouts within the sand-shinnery oak landscape. Populations are not equally divergent across the range and examining the patterns of genetic differentiation with respect to inferred demographic parameters, habitat availability, and suitability helps to elucidate the roles of evolutionary history and current connectivity.

The few variable sites among mitochondrial haplotypes in *S. arenicolus* sampled from throughout the range suggest a relatively recent common ancestor for populations of this species. The Mescalero and Monahans sand dune systems were deposited in the late Pleistocene and early Holocene (11,000–7,500 ybp) in the Pecos River Valley (Green 1961; Hawley et al. 1976; Holliday 2001). It is well established that *S. arenicolus* evolved from within the *graciosus* group (Wiens and Reeder 1997; Frabotta 2002); two evolutionary hypotheses regarding the nature and timing of the divergence between *S. arenicolus* from *S. graciosus* and the colonization of this region may explain the low levels of sequence divergence and the overall patterns of genetic structure among populations of *S. arenicolus*. Kerfoot (1968) suggested that the divergence of *S. arenicolus* from *S. graciosus* preceded the formation of the sand-shinnery oak habitat and that range contraction and habitat specialization occurring at the end of the Pleistocene resulted in the currently restricted distribution of *S. arenicolus*. Alternatively, divergence and specialization of *S. arenicolus* from *S. graciosus* may have occurred more recently in concert with the formation of Mescalero and Monahans sand dunes and subsequent warming and drying of the region. Under the former hypothesis, we expect to find evidence of demographic stability within *S. arenicolus*, particularly if range contraction was not severe. In contrast, a genetic signature of population expansion would support a recent origin of *S. arenicolus* following the colonization of the newly formed sand-shinnery oak habitat.

Although we resolved three genetic groups corresponding to northern, central, and southern portions of this species' range, we were not able to unambiguously resolve the historical patterns of divergence among these groups given our data. The relative coalescent based divergence times from IM analysis of the mtDNA data suggested that the northern population is the youngest of the three groups (Fig. 6) and F_S weakly indicated population expansion in the northern regions with demographic stability in the central and southern regions. The southern regions may have been relictual populations at the end of the Pleistocene, with a subsequent recolonization and population expansion to the northern portion of the range. These results support the hypothesis that the divergence of *S. arenicolus* from *S. graciosus* ancestors probably began early during the formation of the sand-shinnery oak landscape with much more recent population expansion. *Sceloporus graciosus*, the generalist congener of *S. arenicolus* occupies a number of habitat types, including sand dunes in the Pahvant Valley of Utah (Stuart 1932). The

S. graciosus clade from which *Sceloporus arenicolus* diverged may have occupied other sandy habitats in existence prior to the formation of the Mescalero and Monahan sand dunes thereby facilitating specialization and restriction to sand-shinnery oak habitat. Identifying which ecological or geographic forms of extant *S. graciosus* are most closely related to *S. arenicolus* may help to elucidate the historical context of this divergence.

Within *S. arenicolus*, the three groups supported by mtDNA and microsatellite data correspond to geological and ecological landscape features and known distribution breaks indicating long-standing barriers to gene flow in this species. Their range extends to the northeast and southeast along the base at the western edge of a caliche caprock of the Llano Estacado plateau (Fig. 1). Genetic differentiation among the northern and central populations matches discontinuities in suitable habitat and patterns of occurrence supporting limited gene flow in habitat specialists imposed by landscape heterogeneity (Fitzgerald et al. 1997; Branch et al. 2003). Human-altered landscapes in the region include mesquite hummock landscapes, caliche road construction associated with oil and gas development, and flat areas that were cleared for farming and later colonized by shinnery oak. Short-grass prairie, tall-grass prairie, and the human-altered landscapes are unsuitable habitat types for *S. arenicolus* and have led to the genetic divergence of the northern sites from the central sites. Individuals from the southern sites were well-differentiated from those at central sites despite relatively contiguous sand-shinnery oak habitat throughout this portion of their range. However, the intervening area coincides with the westernmost extent of the caprock (Fig. 1) that constricts suitable habitat at the base of the plateau to a narrow north-south band approximately 8 km wide. *Sceloporus arenicolus* do not occur within this area (Fitzgerald et al. 1997), thus, this genetic split is also in line with a potential break in the species' current distribution.

The patterns of genetic structure we found among populations within each of these regions corroborated our findings at larger scales of generally reduced movement and connectivity in *S. arenicolus*. Landscape characteristics can be more important to patterns of isolation than geographic distance particularly when habitat is spatially heterogeneous (Michels et al. 2001; Arnaud 2003; Storfer et al. 2007). The grassland and mesquite dominated landscapes that presumably contributed to differentiation between northern and central populations of *S. arenicolus* are also likely to be responsible for among population differentiation we recovered within these regions. Pairwise F_{ST} values among the four populations of the northern and central regions were high compared to those among the three southern populations (Table 2) despite the larger geographic distances among southern sites, indicating that both natural and anthropogenic habitat fragmentation may have already impacted levels of gene flow. Patches of unsuitable habitat are smaller in the southern portion of the range and this may contribute to increased population connectivity at the local scale.

Variability in patterns of differentiation and levels of genetic diversity may additionally reflect demographic differences resulting from habitat characteristics and fragmentation. Populations on the periphery of a species' range usually have lower effective population sizes because habitat quality is often marginal away from the center of the range (Edenhamn et al. 2000; Vucetich and Waite 2003). Similarly, bottlenecks and founder events can reduce genetic diversity within populations and contribute to higher than expected levels of interpopulation differentiation (Wade and McCauley 1988). Among northern and central localities, the two eastern sites were nearly invariable at mtDNA regions (Fig. 2), with additionally low allelic diversity at microsatellite loci (Site 20 and Site 106, Fig. 4). These localities are the northeasternmost populations in the range at slightly higher elevation and physically isolated from other sites by unsuitable habitat. Small effective population sizes, recent founding events, or reduced population sizes due to local extinction may result from low habitat suitability and patch isolation and may contribute to the low genetic diversity and pronounced population genetic structure of these populations. In contrast, among populations inhabitating larger tracts of continous sand-shinnery oak habitat near the interior of the range, we found greater genetic diversity and some evidence of population connectivity. Bayesian analysis of microsatellite data in Structure revealed limited gene flow between western northern and central populations (Kenna and Camp) and from the southern populations into the western central population (Camp, Fig. 5). Potentially larger effective population sizes and higher habitat quality at these sites may allow for the persistence of genetic diversity and some gene flow despite pronounced population differentiation.

Sceloporus arenicolus is found only in sparsely vegetated sand dune blowouts within the sand-shinnery-oak landscape. Individuals show a strong preference for large, deep blowouts with intermediate sand grain coarseness (Fitzgerald et al. 1997). We hypothesized that specialization to this patchily distributed habitat would restrict movement and result in high levels of genetic structure at fine spatial scales; however, we did not detect any fine-scale genetic structure with spatial autocorrelation analyses. Spatially explicit theoretical models have shown that species of intermediate dispersal ability may experience increased connectivity in temporally and spatially dynamic landscapes because the rearrangement of the habitat patches may connect previously isolated populations (Matlack and

Monde 2004; Wimberly 2006). Common examples of discordance between hypothesized landscape influences and patterns of genetic structure can be found in freshwater fishes where events such as stream captures or drainage rearrangements with topographic changes can result in altered patterns of genetic connectivity (Poissant et al. 2005). Sand dunes are also a dynamic habitat system and the quality and distribution of blowouts can shift rapidly due to wind and rain (Holliday 2001; Muhs and Holliday 2001). The non-static nature of the sand-shinnery oak landscape is also likely to contribute to historical patterns of connectivity and gene flow among populations that are now isolated (Wimberly 2006). Changes to habitat connectivity within the sand-shinnery oak landscape over short time scales may prevent the loss of genetic diversity by increasing effective population size. Currently, a large part of the Mescalero sand dunes are inactive (i.e. non-shifting) and semi-stabilized; however, the Monahans sand dunes in Texas and other sites with active dunes scattered throughout the range of *S. arenicolus* are continually altered by wind moving from west to east along the base of the Llano Estacado plateau (Holliday 2001; Muhs and Holliday 2001). If dune activity does promote gene flow at fine scales within the southern region, genetically distant mtDNA haplotypes found there (Fig. 3) may represent persistent ancestral diversity maintained through greater overall effective population sizes. Alternatively, these haplotypes may result from unidirectional dune-mediated gene flow at the range-wide scale from northern and central regions.

Understanding the scale of genetic structure and how it is related to landscape characteristics helps us predict how anthropogenic modifications will impact populations of this endemic habitat specialist. Oil and gas development and the application of tebuthiuron herbicides to kill shinnery oak for range management cause the fragmentation of existing habitat, alter the network of habitat patches, and disrupt the geomorphological processes that maintain the sand-shinnery oak landscape. Shinnery oak removal results in a modified landscape with reduced topographic relief and smaller and fewer blowouts. Our study sites formerly occupied by *S. arenicolus* that were subjected to shinnery oak removal in 1988 show little signs of recovery and have not been re-colonized by *S. arenicolus* (pers. obs.). *Sceloporus arenicolus* requires sand dune blowouts of particular characteristics for reproduction, foraging, and thermoregulation (Degenhardt et al. 1996; Fitzgerald et al. 1997; Snell et al. 1997). Reductions in patch abundance and quality are likely to also affect population vital rates such as survivorship, growth, and fecundity (Hokit and Branch 2003a,b) that, in turn, will decrease effective population sizes and levels of connectivity. Given the high levels of differentiation we found among and within the three regions and low population structure at finer spatial scales, the specific arrangement of sand dune blowouts within a dune complex is not as critical to the persistence of *S. arenicolus* as is the quality and availability of blowout complexes across the Mescalero sands and Monahans sands region. Patch characteristics influence population densities and effective population size, thereby affecting resistance to local extinction in this dynamic landscape. The overall variability among populations in levels of genetic diversity indicates genetic processes are not equivalent across the landscape and that habitat specialists may be particularly sensitive to patch characteristics and dynamics within these heterogeneous landscapes.

Although we did not detect fine-scale genetic structure in association with human disturbances, we cannot discount the potential impact of recent anthropogenic activities on local gene flow in *S. arenicolus*. First, it is possible that *S. arenicolus* populations have not had sufficient time to reflect the effects of recent habitat alteration at fine scales. Second, shinnery oak destruction and landscape alteration (Snell et al. 1997) are likely to decrease levels of genetic diversity even if populations do persist through a reduction in population size. The absence of *S. arenicolus* from many presumably suitable sites (Fitzgerald et al. 1997), the sharp genetic break between central and southern regions despite the presence of sand-shinnery oak habitat, and the low genetic diversity of some, but not all populations underscore the fact that unrecognized characteristics of the landscape may also be important to habitat connectivity and population persistence. Our data suggest that although the network of blowouts within a dune complex may not need to be managed at fine scales, the preservation of large areas containing a network of dune complexes with large blowouts is necessary to maintain historical levels of connectivity, prevent local extinction, and avoid the loss of genetic diversity due to genetic drift in reduced populations. Furthermore, our deeper analysis of the evolutionary history of the Dunes Sagebrush-Lizard indicates high divergence among three clades as well as among the populations within them. Thus, conservation efforts should focus not only on the preservation of dune complexes, but their preservation within each of these geographic regions. Whether the lack of gene flow among these groups is corroborated by ecology, morphology, or behavior is not yet known, but would provide important data for captive breeding, reintroductions, and the determining the overall uniqueness of each group. Such future endeavors will further contribute to the effective conservation of this endemic habitat specialist.

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