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CONSERVATION GENETICS OF THE ENDANGERED COACHELLA VALLEY FRINGE-TOED LIZARD (*UMA INORNATA*)

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ABSTRACT: We used microsatellite loci to examine rangewide population structure and interpopulation gene flow in the federally threatened Coachella Valley fringe-toed lizard (*Uma inornata*). Our results indicate low population differentiation consistent with high gene flow, recent colonization and range expansion, and/or frequent local extirpation/recolonization events. Given high historical gene flow among populations and current isolation of remaining populations, conservation planning for this species should include monitoring of potential deleterious effects that may result from reduction in gene flow, such as inbreeding and loss of genetic variation, to ensure maintenance of ecological and evolutionary population processes adequate for long-term survival of the species.

Key words: Fringe-toed lizards; Gene flow; Genetic variation; Microsatellites; *Uma inornata*

THE THREE species of fringe-toed lizards in the genus *Uma* have unique adaptations for sand dune habitats, including specialized toe scales for locomotion (Carothers, 1986; Luke, 1986), ear scales to block blowing sand, a dorso-ventrally flattened body and wedge-shaped head for sand burrowing, and specialized nostrils for breathing while submerged in the substrate (Norris, 1958; USFWS, 2000). The Coachella Valley fringe-toed lizard, *Uma inornata*, is the species in this genus with the smallest distribution, historically occupying approximately 171,000 acres of dune habitat in the Coachella Valley, Riverside County, California, U.S.A. (California Dept. Fish and Game et al., 2004). Widespread habitat modification for agricultural and urban development in the Coachella Valley has fragmented once continuous habitat (Fig. 1) and altered both the rate of input, renewal, and size of wind-born sand particles required for the persistence of the dune systems (Barrows, 2000; Turner et al., 1984). Unfortunately, specialized morphology and behavior make *U. inornata* extremely vulnerable to changes in dune composition and structure (Barrows, 1997; Turner et al., 1984). As a result of anthropogenic habitat modification, *U. inornata* is currently classified as threatened by the U.S. government (USFWS, 1980) and endangered by the State of California (California Dept. Fish and Game, 2000), and is restricted to isolated patches covering less than 16% of original dune habitat (California Dept. Fish and Game et al., 2004). The effect this reduction and fragmentation of habitat will have on the genetic variability and long-term evolutionary persistence of *U. inornata* populations depends in part on the historical rates of gene flow among these populations and the degree of population structure.

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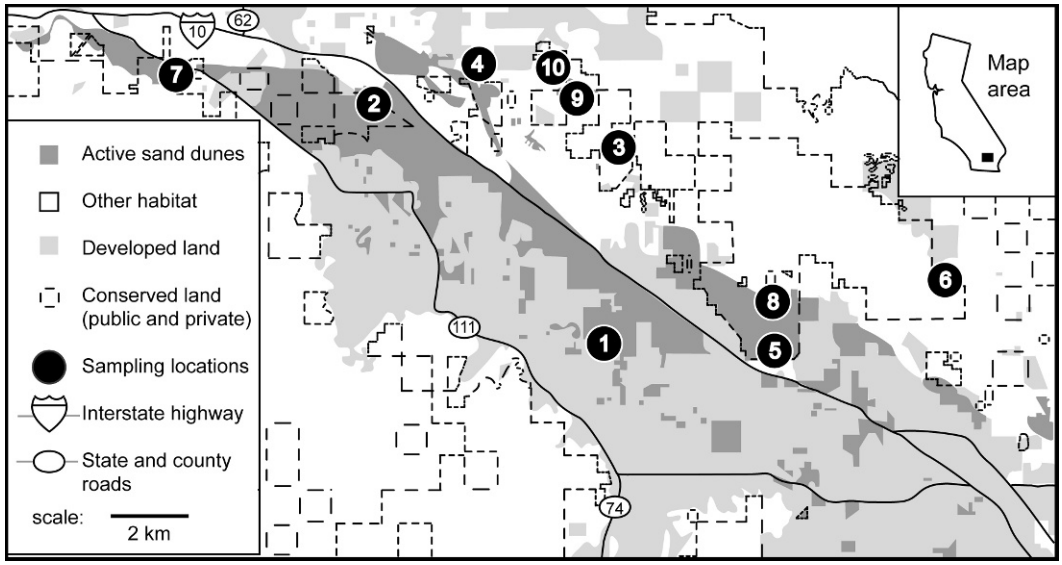

FIG. 1.—Map of the Coachella Valley, Riverside County, California, with active dune habitat, developed land, and conserved land (adapted from California Dept. Fish and Wildlife, 2004). Collection localities for the *Uma inornata* included in this study are 1 = Anneberg, 2 = Whitewater River Reserve, 3 = Coachella Valley Preserve South, 4 = Willow Hole Preserve, 5 = A-1 Aggregate, 6 = Eastern Indio Hills, 7 = Windy Point, 8 = Coachella Valley Preserve North, 9 = Sleeping Man Dunes, 10 = Sleeping Man Dunes North. Unshaded areas labeled "other habitat" are composed primarily of desert scrub.

To date, conservation efforts have necessarily focused on preserving habitat critical to this species' survival. In 1985, the U.S. Fish and Wildlife Service, in conjunction with state and private parties, set aside a total of 20,114 acres to protect approximately four percent of *U. inornata*'s original dune habitat and the putative source of dune sand (Barrows, 1996; USFWS, 2000). Given the continued threat to surviving populations, a Coachella Valley Multiple Species Habitat Conservation Plan/Natural Community Conservation Plan (hereafter referred to as the conservation plan) was developed to coordinate conservation efforts across species and ecosystems (California Dept. Fish and Game et al., 2004). The final 2004 administrative draft recommends increasing the acreage of protected core habitat for *U. inornata*, preserving the ecological processes that form dune systems, and maintaining the "evolutionary potential" of lineages within this species (California Dept. Fish and Game et al., 2004). However, the conservation plan does not explicitly consider the underlying population genetic structure of the target species. Maintaining genetic structure and levels of intra-population genetic variation could be crucial to designing an appropriate conservation strategy that maintains a species' evolutionary potential. For example, species with low genetic structure (high gene flow among populations) can be more susceptible to inbreeding depression when isolated by habitat fragmentation than populations that are historically inbreeding (Elgar and Clode, 2001). Information about historical population structure can therefore be used to evaluate the current conservation plan. Populations of *U. inornata* could have historically high levels of gene flow due to migration of individual lizards or due to the historically dynamic nature of wind-mediated movement of sand dunes across the valley. In that case, maintenance of the species may require habitat corridors or even translocation of animals to prevent the deleterious effects of inbreeding once gene flow is interrupted. Conversely, the high degree of dune specialization could have historically isolated individual populations, rendering them less susceptible to inbreeding. In this case, efforts should focus on maintaining population numbers and conserving isolated populations, each of which may be

TABLE 1.—Sampling localities, sample sizes, and field collection numbers for all *Uma inornata* included in this study. Site numbers correspond to those in Figure 1.

Site #	Site name	# samples	Tissue number
1	Anneberg	6	CAP 1701–1704; CAP 1706–1707
2	Whitewater River Reserve	15	CAP 1708–1722
3	Coachella Valley Preserve South	12	CAP 1723–1734
4	Willow Hole Preserve	8	CAP 1735–1742
5	A-1 Aggregate	3	CAP 1743, 1745–1746
6	Eastern Indio Hills	5	CAP 1747–1751
7	Windy Point	8	CAP 1752–1759
8	Coachella Valley Preserve North	11	CAP 1760–1770
9	Sleeping Man Dunes	7	CAP 1771–1777
10	Sleeping Man Dunes North	1	CAP 1778

locally adapted to particular environmental conditions.

Previous genetic work on *U. inornata* has focused on taxon status (Adest, 1977; Trépanier and Murphy, 2001). Morphological (Norris, 1958), allozyme (Adest, 1977), and mitochondrial DNA sequence data (Trépanier and Murphy, 2001) suggest *U. inornata* diverged relatively recently from its sister taxon, *U. notata*. However, sampling in these studies was not sufficient to examine structure among populations throughout the Coachella Valley. Here we use fast-evolving microsatellite markers and more extensive sampling to identify the extent of population differentiation and structure in *U. inornata*. Because we are sampling an endangered species whose numbers have been reduced by habitat loss, our sample sizes from each location within the Coachella Valley are relatively low. Nevertheless, our analysis allows us to estimate historic gene flow among populations and explore levels of genetic diversity and structure rangewide. These estimates are critical to designing a conservation and management plan that actively incorporates maintenance of evolutionary processes.

MATERIALS AND METHODS

Sample Collection

Samples were collected from 10 sites within the Coachella Valley in Riverside County, CA, U.S.A. (Fig. 1; Table 1): Anneberg ($n = 6$), Whitewater River Reserve ($n = 15$), Coachella Valley Preserve South ($n = 12$), Willow Hole Preserve ($n = 8$), A-1 Aggregate north of Thousand Palms ($n = 3$), Eastern Indio Hills ($n = 5$), Windy Point ($n = 8$), Coachella Valley Preserve North ($n = 11$), Sleeping Man Dunes ($n = 7$) and Sleeping Man Dunes North ($n = 1$). In all analyses, the single individual collected at Sleeping Man Dunes North was grouped with those collected from Sleeping Man Dunes. Lizards were captured by hand or with nooses. Blood samples were collected from the infraorbital sinus, and animals were released at their point of capture. Total genomic DNA was isolated from blood samples by digestion with cell lysis buffer and Proteinase K, followed by a standard phenol-chloroform organic clean up (Sambrook and Russell, 2001).

Microsatellite Amplification

We were unable to develop and screen a microsatellite library specific to *Uma inornata*; therefore, we tested microsatellite primer pairs developed for other iguanid lizard species for amplification and polymorphism. Three loci developed for *Uta* (MCC, PLkn, and SVeg; Zamudio and Sinervo, 2000) and one developed for *Sceloporus jarrovii* (Scel82; Zamudio and Wieczorek, 2000) successfully amplified polymorphic loci in *U. inornata*. We amplified each locus in 10 μl total reaction volumes; each PCR reaction included 1X buffer, 0.125 mM of each dNTP, 0.5 uM forward and reverse primers, 0.25 U Taq DNA polymerase, and either 0.25 mM $MgCl_2$ (MCC and PLkn) or 0.10 mM $MgCl_2$ (SVeg and Scel82). Initial denaturing was set at 94 C for 10 min, followed by 30 to 35 cycles of 94 C for 45 s, 55 C (MCC and PLkn) or 50 C (SVeg and Scel82) for 1 min, and 72 C for 1 min, and a single final extension of 72 C for either 5 min (MCC and PLkn) or 30 min (SVeg and Scel82). Samples were electrophor-

ESED on an ABI Prism 377 Automated DNA Sequencer and sized with 500 TAMRA size standard using Genescan v. 3.1 and Genotyper v. 2.5 (Applied Biosystems, Foster City, CA).

Deviations from Equilibrium

We estimated significant deviations from Hardy-Weinberg equilibrium (HWE) in ARLEQUIN v.2.0 (Schneider et al., 2000) using a Markov chain of length 10^7 with 1000 dememorization steps. We also used ARLEQUIN to test for linkage (or gametic) disequilibrium (LD), the nonrandom association of alleles from different loci for each sampling location. The ratio of the likelihoods of the data under models excluding and allowing LD was calculated by permuting the data 1600 times using 500 initial conditions (Slatkin and Excoffier, 1996). Significance was determined by using the more conservative chi-squared test (Lewontin and Felsenstein, 1965) and the more powerful Fisher's exact test (Slatkin, 1994).

Microsatellite data can be confounded by null alleles (an allele with a mutation in the flanking region which prevents PCR amplification). An individual heterozygous for a visible and a null allele would be inaccurately scored as homozygous for the visible allele. High frequencies of null alleles within a population could affect calculations of all population measures. We calculated the frequency of null alleles using the method of Brookfield (1996).

Measures of Population Structure

We used several methods to estimate the degree of population structure. We calculated pairwise F_{ST} values based on haplotype frequencies (Reynolds et al., 1983) and Nei's average number of pairwise population differences (Nei and Li, 1979), using ARLEQUIN (Schneider et al., 2000). The statistical significance for the estimated genetic distances was determined by permuting haplotypes 10^5 times between populations to generate a null distribution of no differentiation between populations. Tests of significance were adjusted using a sequential Bonferroni correction for multiple comparisons (Rice, 1989). F_{ST} values were used to calculate M, the absolute number of migrants exchanged between sampling locations (Slatkin, 1993). A Mantel test of matrix correlation was performed between F_{ST} and the physical distances between populations to determine whether differentiation was based on isolation by distance. To test the hypothesis of random distribution of individuals between pairs of populations, we performed global and pairwise exact tests of sample differentiation based on haplotype (Goudet et al., 1996; Raymond and Rousset, 1995). In addition, ARLEQUIN was used to calculate the likelihood that each individual genotype would be found in each population (Paetkau et al., 1995, 1997; Waser and Strobeck, 1998).

As a final method of examining population structure, we used Bayesian model-based clustering methods to estimate the posterior probability of the number of populations (K), implemented in the programs STRUCTURE v.2 (Pritchard et al., 2000) and BAPS v. 3.1 (Corander et al., 2003). STRUCTURE estimates the posterior probability of K populations, and for each individual lizard, the probability of membership in a specific population. Two models of differentiation were used: an admixture model and a linkage admixture model. In the first, admixture is permitted between populations, such that individual lizards can have mixed ancestry (Pritchard et al., 2000). In the second, admixture can lead to linkage disequilibrium (Falush et al., 2003). We computed posterior probabilities of K given 1 through 9 populations after an admixture burn-in period of 10^6, an additional burn-in period of 10^6, and a run after burn-in of 10^6. Large estimates of K suggest reduced gene flow and distinct genetic demes, while low estimates suggest high gene flow between sampled locations. BAPS estimates the posterior distribution of the number of clusters in a sample, and the membership of each cluster. Five analyses were run using 20 as the prior for K, and three were run using priors of even numbers from 2 through 40, with default parameters. Reduced gene flow would result in clusters composed of individuals from the same sampling locality, while high gene flow would result in few clusters, or clusters with highly mixed membership.

TABLE 2.—Observed (H_o) and expected (H_e) heterozygosities and mean number of alleles for individual populations and for the entire sample of *Uma inornata* genotyped for this study.

	Locality number									
	1 (n = 6)	2 (n = 15)	3 (n = 12)	4 (n = 8)	5 (n = 3)	6 (n = 5)	7 (n = 8)	8 (n = 11)	9 + 10 (n = 8)	all (n = 76)
MCC										
H_o	0.333	0.600	0.250	0.750	0.667	1.00	0.500	**0.200**[1]	**0.250**[1]	**0.467**[1]
H_e	0.789	0.713	0.377	0.867	0.867	0.689	0.800	0.747	0.850	0.729
PLkn										
H_0	1.000	0.533	0.333	0.500	0.333	0.200	0.375	0.182	0.125	0.395
H_e	0.712	0.497	0.370	0.592	0.333	0.378	0.458	0.481	0.442	0.440
SVeg										
H_o	0.750	0.500	0.500	0.625	0.667	0.000	0.125	0.455	0.250	0.425
H_e	0.750	0.569	0.551	0.592	0.733	0.644	0.125	0.394	0.500	0.494
Scel82										
H_o	0.500	0.462	0.273	0.375	0.333	0.600	0.625	0.364	0.250	**0.408**[1]
H_e	0.429	0.582	0.325	0.425	0.933	0.511	0.542	0.606	0.342	0.478
Mean number alleles/locus	3.25	4.00	3.50	3.50	2.50	2.50	2.75	2.75	2.50	5.75

[1] = statistically significant deviation from Hardy-Weinberg proportions ($P < 0.01$).

To detect recent reduction in effective population size across all populations, we used the program BOTTLENECK (Piry et al., 1999). BOTTLENECK uses allele frequencies to examine whether expected heterozygosity (H_e) is significantly higher or lower than that expected at a constant-size population equilibrium (H_{eq}). The program utilizes three statistical tests, but only the Wilcoxon sign-rank test has sufficient strength to detect differences given our sample size and number of loci (Cornuet and Luikart, 1996). There were not enough samples per site to perform the test on individual locations, only on all sampled populations combined. Probabilities were run under a two-phased model of mutation (TPM), which assumes primarily a one-step mutation model, and a small percentage (5%) of multiple-step changes in microsatellites. To determine if there are a significant number of loci with heterozygosity excess or deficit, BOTTLENECK computes the probabilities that loci meet the expected heterozygosity at mutation-drift equilibrium assuming constant population size.

RESULTS

In total, we genotyped 76 individuals from 9 populations. Most sites conformed to Hardy-Weinberg proportions (Table 2). However, locus MCC deviates from HWE at Coachella Valley Preserve North (site 8) and Sleeping Man Dunes (site 9 + 10). Across all locations, locus MCC and locus Scel82 had lower observed heterozygosity than expected under HWE.

Two individuals did not amplify for locus Scel82, which may indicate the presence of a null allele. If deviations from expected heterozygosities were due to the presence of null alleles alone, the frequency of the null alleles (Brookfield, 1996) would be 0.219 for MCC and 0.079 for Scel82. No individuals failed to amplify at locus MCC. Therefore, it is unlikely that the observed deviation from HWE at locus MCC are due to null alleles alone.

Linkage disequilibrium was detected in Anneberg (site 1) between loci SVeg and Scel82, MCC and SVeg, and MCC and Scel82. Willow Hole Preserve (site 4) showed linkage disequilibrium between MCC and SVeg. Over all samples combined, linkage disequilibrium was detected between MCC and PLkn and SVeg and Scel82 (Table 3).

Population Structure

After sequential Bonferroni correction (Rice, 1989), conventional pairwise F_{ST} values based on haplotype frequencies were significant between Coachella Valley Preserve South (site 3) and Willow Hole Preserve (site 4) populations (Table 4, above the diagonal). F_{ST} values calculated using pairwise distances were significantly different between Coachella

TABLE 3.—Linkage disequilibrium tests between pairs of loci across all populations sampled.

	LOCUS		
	MCC	SVeg	Scel82
SVeg	locality 8[1,2]		
Scel82	locality 1[3,4], locality 4[1,2]		
PLkn	locality 1[1,2], all localities[1]	locality 8[3,4]	locality 1[3,4]

[1] exact $P < 0.05$
[2] chi square $P < 0.05$
[3] exact $P < 0.01$
[4] chi square $P < 0.01$

Valley Preserve South (site 3) and three populations: Whitewater River (site 2), Eastern Indio Hills (site 6), and Windy Point (site 7) (Table 4, below the diagonal). A matrix correlation analysis (Mantel test) was performed between F_{ST} values and the geographic distances between populations to test for isolation by distance. After 10^6 permutations, the determination of Y (F_{ST} value) by X1 (distance) was 0.094 ($P = 0.357$), indicating that isolation by distance did not play a significant role in causing differentiation. Mantel tests for isolation by distance were also performed on Slatkin's linear F_{ST}, log-F_{ST}, log-M and log-genetic distance, and none of these distance measures showed a significant pattern of IBD ($P > 0.05$). One problem with conventional F_{ST} is that the calculations assume populations are at equilibrium (Hedrick, 2000), an assumption to which natural populations rarely conform.

The global exact test of differentiation based on haplotype frequencies was not statistically significant ($P = 0.44017 +/- 0.09226$), neither were the pairwise comparisons ($P > 0.05$). Further support for nondifferentiation among populations comes from the calculation of the likelihood of an individual coming from each population. Between 25 and 60% of individuals genotyped had a higher likelihood of assignment to a different population than their population of origin. An exception to this pattern was population A-1 Aggregate (site 5), for which all three individuals were correctly assigned to the locality where they were collected. Estimates of the absolute numbers of migrants between populations were all high (Table 5), indicating historical panmixia among most populations throughout the Coachella Valley.

The Bayesian analyses of population structure further suggests panmixia among populations. Under all models, STRUCTURE determined the data best fit the prior of K = 1 populations [$Pr(K = 1) = 1.0$], although under the admixture model a prior of $K = 2$ resulted in a relatively high probability [$Pr(K = 2) = 0.9880$]. However, individuals did not partition strongly into two clusters: the highest probability that any individual belonged in one population was 0.515, and *a priori* defined sampling locations had between 0.496 and 0.509 individuals belonging to one or the other cluster. The parameter alpha, which

TABLE 4.—Pairwise F_{ST} between nine populations of *Uma inornata*. Above the diagonal = conventional F_{ST} based on haplotype frequencies. Below the diagonal = F_{ST} based on pairwise difference.

	Locality number								
	1	2	3	4	5	6	7	8	9 + 10
1	0	−0.0045	0.0584	−0.0236	−0.0502	−0.0189	−0.0037	−0.0071	−0.0202
2	0.0084	0	0.0544	0.0193	0.0222	0.0192	0.0127	0.0079	0.0041
3	0.1305	**0.1055**[1]	0	0.1230	0.1277	0.0986	0.0950	0.0474	0.0420
4	−0.0376	0.0448	0.1188	0	−0.0359	−0.0073	0.0226	0.0308	0.0187
5	−0.0135	0.0755	0.1387	−0.0246	0	0.0195	0.0280	0.0272	0.0280
6	0.0789	0.0812	**0.1742**[1]	0.0040	−0.0092	0	−0.0183	0.0327	−0.0322
7	0.1178	0.0469	**0.2577**[1]	0.1407	0.1425	0.0802	0	0.0134	0.0033
8	0.0388	−0.0037	0.0724	0.0638	0.0555	0.0704	0.0332	0	0.0163
9 + 10	0.0748	0.0862	0.1291	0.0325	0.0566	0.0094	0.1625	0.0952	0

[1] significant after sequential Bonferroni correction, $P < 0.05$.

TABLE 5.—Numbers of migrants per generation between pairs of populations throughout the range of *Uma inornata* estimated using F_{ST} (Slatkin, 1993).

	Locality number							
	1	2	3	4	5	6	7	8
2	infinite							
3	4.2677	3.8428						
4	infinite	11.7390	3.5240					
5	infinite	5.2895	4.6455	infinite				
6	9.1834	5.9583	2.3698	23.4706	infinite			
7	4.4721	11.2143	1.4401	2.8696	2.3411	5.7328		
8	30.0779	infinite	6.4030	6.8091	8.6965	6.6014	14.5717	
9 + 10	9.4160	5.4537	3.3719	17.4867	139.4286	52.5277	2.5778	4.7514

describes the Dirichlet distribution of the ancestry proportion for each individual failed to converge even after a burn-in of 10^{14}. This may be due either to an absence of population structure or insufficient data in our sample (Pritchard et al., 2000). The BAPS analysis suggested 10–11 clusters, depending on the run. These clusters were highly mixed with individuals from multiple sampling locations and inconsistent composition between runs, suggestive of panmixia.

Our genetic analyses using the program BOTTLENECK did not find evidence of a severe species-wide bottleneck. We could not reject the null model that all loci fit the heterozygosity expected at a constant-size equilibrium (heterozygote deficiency alone: $P = 0.06250$; heterozygote excess alone: $P = 0.96875$; heterozygote excess or deficiency: $P = 0.12500$).

DISCUSSION

A major goal of conservation is to maintain the ecological and evolutionary processes that permit long-term persistence of threatened or endangered species. Relevant evolutionary processes include migration of individuals across a landscape and persistence of sufficient genetic variation within and among populations. Gene flow can prevent inbreeding depression in organisms for which inbreeding is a problem (Keller and Waller, 2002), and the maintenance of genetic variation is crucial for continued adaptation to shifting environments (Hedrick, 1996). We evaluate the historical importance of these processes in the endangered lizard *Uma inornata*.

Genetic variability of *U. inornata* appears low in this study, corroborating results from rangewide assays in previous studies (Table 2; Adest, 1977; Trépanier and Murphy, 2001). Although our sample sizes were small per population, we did sample across their entire range. If genetic variability were high, this sampling scheme should still reveal differences in allele frequencies among populations. Our analyses suggest little to no population differentiation. Historic gene flow estimates between sampling sites across the Coachella Valley are high (Table 5), suggesting that prior to human–mediated fragmentation of habitat, the species was panmictic with pervasive gene flow throughout the valley. However, metapopulation dynamics could also cause this observed low differentiation between populations. If *U. inornata* formed a metapopulation, homogenization of genetic diversity would result from recolonization of an area by individuals from neighboring populations after a local extirpation event, and a continual renewal of newly derived alleles in populations receiving immigrants.

We evaluate three possible processes that could result in low variability in *U. inornata*: (1) human-mediated population bottlenecks (Trépanier and Murphy, 2001), (2) recent range expansion (Slatkin, 1993), and (3) metapopulation dynamics (Hedrick, 1996). Low variability and differentiation due to human-mediated bottlenecks is unlikely, because we did not detect the signature of a recent reduction in effective population size. There is little doubt that habitat reduction has critically reduced *U. inornata*'s population size compared to historical numbers (USFWS, 1980). However, for human-mediated bottlenecks to cause the observed low variability, the entire species would have to have been

reduced to a single population which subsequently and very recently spread across the valley. In the Coachella Valley, gradual habitat disturbance is more likely to have affected individual populations at different times.

Uma inornata is hypothesized to have spread into the Coachella Valley at the time of its divergence from *U. notata* (Norris, 1958; Trépanier and Murphy, 2001). Our data support this hypothesis, as we detected large values of migration between populations (Table 5) and no pattern of genetic isolation by distance, both characteristics of a recent range expansion (Slatkin, 1993). These patterns are also expected for panmixia, and on the basis of our data we cannot distinguish between recent range expansion and panmixia. Historically, dune habitat did occur across the entire Coachella Valley. Nonetheless, dunes tend to be semi-isolated from one another (Norris, 1958; Trépanier and Murphy, 2001), limiting movement of individual lizards across large parts of the species' range. Fringe-toed lizards have small home ranges, of about 1070 m^2 for males and 440 m^2 for females (Horchar, 1992), and thus may not be likely to migrate over long distances at a level sufficient for panmixia.

Genetic and observational data suggest that metapopulation dynamics drive both low variability and low differentiation in *U. inornata*. In a metapopulation, local extirpation and recolonization of small populations can be relatively common. Our study detected linkage disequilibrium between some pairs of loci (Table 3), an effect that can be generated by a small founder population (Hedrick, 2000). In addition, at the Coachella Valley Preserve North (site 8), one locus departed from HWE (Table 2), which could also be explained by a recolonization event with a small founder population. Observational evidence is suggestive of a metapopulation - isolated dunes have suffered local extirpations (C. Barrows, personal observation, as cited in California Dept. Fish and Game et al., 2004), and population numbers of *U. inornata* regularly decline after drought, only to rebound in following years (Barrows et al., 1995; Muth and Fisher, unpublished data as cited in California Dept. Fish and Game et al., 2004). It is difficult to know whether this pattern of population fluctuation and possible local extirpation reflects historical population dynamics or whether human-mediated fragmentation of habitat has led to edge effects and greater sensitivity to environmental perturbation. If these demographic fluctuations are natural in this system, it seems likely that extinct populations could historically have been rescued by dispersal, given the connection among populations and the widespread distribution of populations in all dunes of the valley.

The conservation plan for this region (California Dept. Fish and Game et al., 2004) addresses maintenance of genetic variability in *U. inornata* by maximizing the size and number of preserved areas, given the demands of cities and agriculture in the Coachella Valley. The plan also attempts to restore or prevent reduction of habitat quality by targeting such negative effects as off-road vehicle use and invasive species. These efforts should in fact increase or maintain both population size and the number of populations, thus reducing loss of genetic diversity.

It is more difficult to address maintenance of extensive gene flow or the metapopulation dynamics which seem to have characterized this system historically. These processes depend on the ability of *U. inornata* to move among populations within the Coachella Valley. The conservation plan recommends the establishment of corridors between preserves, including wildlife undercrossings at major roads (California Dept. Fish and Game et al., 2004). Unfortunately, the mechanism of natural migration or recolonization is not known in *U. inornata*. In addition to direct movement among populations by dispersing individuals, passive migration via the dynamic rearrangement of shifting sands may have served as transport vectors across the valley (Norris, 1958). Dunes along the western edge of the Salton Sea, in the same basin as the Coachella Valley, have been estimated to move as much as seven meters per year, although larger dunes can be completely stationary (Norris, 1958). Isolated populations could have been brought into contact, or a local habitat recolonized, when dunes merged by wind activity. If gene flow was mediated by dune movement rather than by movement of individuals, maintaining natural

population dynamics may be difficult without more drastic habitat protection or artificial translocation of individual animals. However, translocation of reptiles has uncertain success (e.g., Dodd and Seigel, 1991; Reinert, 1991; Sullivan et al., 2004) and ignores possible effects on undetected local adaptation. In addition, while gene flow of one migrant per generation among geographic areas has been used as a rule of thumb by managers to achieve a balance between local adaptation and maintenance of variation (Allendorf, 1983; Frankel and Soulé, 1981), this general rule may not be equally appropriate for all species (e.g., Varvio et al., 1986). Our analyses do not indicate how many migrants would be appropriate to maintain historical processes. Therefore, we do not recommend human-mediated movement of individuals to promote gene flow without additional behavioral data.

To design a strategy appropriate for a particular species, conservation managers need to understand key species characteristics, such as dispersal patterns (that affect population connectivity) and mating system (that affects population genetic variability). Unfortunately, this information may be difficult to obtain, especially once a species is identified as threatened or endangered and ecological and evolutionary processes have been disrupted. Population genetic studies cannot replace behavioral or ecological studies, but they can provide insight into processes and help guide management decisions. Our data suggest high connectivity and low genetic variability among populations of the Coachella Valley fringe-toed lizard; given these results an additional challenge for the preservation of this species is the maintenance of the processes that maintain the pattern for genetic health of the now isolated populations of *U. inornata*. Ideally, a conservation plan would maintain corridors between existing dune habitats large enough to allow not only individual animal migration, but also the dynamic shifting of entire dunes (Norris, 1958). Given the current level of development in the Coachella Valley, however, the reality is that any conservation strategy will need to be balanced by the needs of human communities in the area. Thus, behavioral studies examining the migration of individual *U. inornata*, in conjunction with further genetic analyses, are a critical next step in determining whether proposed corridors and overall levels of population connectivity are sufficient to maintain natural population genetic dynamics of this species.

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