Persistence and local extinctions of endangered lizard *Uma inornata* on isolated habitat patches

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ABSTRACT: Occupancy and persistence in naturally isolated habitat patches were analyzed to evaluate patterns of local extinction of an endangered species, the Coachella Valley fringe-toed lizard *Uma inornata*. We examined 4 parameters: (1) habitat quality, (2) patch size, (3) patch connectivity, and (4) drought. The Coachella Valley in southern California's Colorado Desert has a strong west–east gradient, with drier and more persistent drought conditions in the east. The distribution of habitats along this gradient was the best single factor explaining patch occupancy over 14 yr. Drought and patch size provided the best multivariate model. When the westernmost habitat patches were analyzed alone, patch size was the only statistically significant variable. Our results show how conservation planning criteria for species of concern can differ within a species' range. In this instance, patches located in the eastern part of the valley may need to be much larger than those in the more mesic west. Applying one minimum habitat size criteria for conservation efforts throughout the lizards' range could result in either not protecting viable populations (e.g. in the west) or spending limited conservation funds on protecting non-sustainable populations in the east (if the minimum size was too small). Identifying gradients that may impact population persistence and extinction across landscapes is an important step in effective conservation planning.

KEY WORDS: Patch size · Persistence · Extinction · Drought · *Uma inornata* · Conservation

INTRODUCTION

An important goal for conservation biology is to provide a scientific basis for informed conservation planning. This background includes identifying habitat loss and extinction thresholds. Some of the variables that may impact population occurrence and persistence on habitat fragments include patch size and the distance between additional habitat patches (Simberloff 1997), the number of habitat patches and the porosity of the inter-patch matrix (Hanski 1991), habitat quality (Thomas 1994, Scott et al. 2006), and various stochastic processes such as drought or fire (Gilpin & Soulé 1986, Wiens 1997). Rather than a single explanatory factor, extinctions are likely the result of some synergistic combination of these variables. The challenge with respect to protecting biodiversity is to identify those variable combinations.

To evaluate variables which alone or in concert contribute to extinctions on habitat fragments, patch size,

distance between patches, as well as a range of factors generally lumped as habitat quality, need to be clearly defined. Oceanic islands are often used as models for evaluating extinctions in terrestrial species; the distinction between habitat patches (the island) and the surrounding matrix (water) can be clearly defined. In mainland terrestrial systems the distinctions between habitat and matrix are often less distinct. Our study system includes well-defined patch-matrix distinctions consisting of aeolian sand habitat patches captured in uplifted alluvial hills. The fine aeolian sand sharply contrasts with the alluvial rock and gravel matrix and so can be readily delineated. This separation is biotic as well as physical. Isolated sand dunes form unique insular habitats (Britton & Rust 1996) that are inhabited by aeolian sand-obligate plants (Pavlick 1985, 1989), mammals (Brown 1973), arthropods (Seely 1978, Rust 1986, Britton & Rust 1996, Barrows 2000), and reptiles, particularly members of the saurian genus *Uma* in North America (Norris 1958, Trépanier & Murphy

2001). In the present study we focused on patterns of persistence and extinction for one of the sand dune obligate reptiles, the Coachella Valley fringe-toed lizard *Uma inornata*, which was listed in 1980 as threatened (US federal) and endangered (State of California).

Aeolian sand habitats once stretched across much of the floor of the Coachella Valley of southern California's Colorado Desert (Beheiry 1964, Proctor 1968), providing a nearly contiguous habitat for a diverse community of aeolian sand-adapted species. Over the past 3 decades, increases in human population and suburban development have resulted in the loss of as much as 95% of this habitat and have severely fragmented what remains (Barrows 1996, 2006). However, not all that fragmentation was the result of anthropogenic actions. The numerous sand-etched rocks or ventifacts indicate that an aeolian sand sheet spread over the western Indio Hills forming the northern margin of the Coachella Valley's dune field (Beheiry 1964, Proctor 1968, Lundstrom 2001). Besides ventifacts, current evidence for a sand sheet includes the occurrence of aeolian sand patches on the leeward side of steep ridges (falling dunes, sensu Lancaster 1995) and in isolated valleys. Although there were likely earlier events, the most recent movement of sand across the Indio Hills followed heavy rains, flooding and fluvial sediment movement in 1937–8 (Griffiths et al. 2002), with subsequent aeolian sand movement in the months and years following that flood. Aerial images taken in 1953 clearly show each of the sand patches in its present location and size. The matrix separating these sand patches consists of steep slopes of uplifted alluvial gravel and rock (Proctor 1968). The temporal and spatial patterns of patch occupancy exhibited by these fringe-toed lizards on these sand patches provide an opportunity to evaluate variables that lead to local extinctions in arid environments.

We tested 4 hypotheses to explain observed lizard extinction patterns on naturally fragmented habitat patches. These hypotheses were: (1) patch size and distance between patches, with an expectation that larger patch size and smaller inter-patch distances would support higher occupancy rates; (2) the number of habitat patches with potential connectivity, with an expected positive correlation with higher patch occupancy; (3) differences in habitat quality to the extent that some sites were unsuitable for occupancy; and (4) differential environmental stochasticity (drought), resulting in temporal and spatial variation in patch suitability. To test these hypotheses we compared observed patterns to predicted patterns for each hypothesis. Habitat quality for Coachella Valley fringe-toed lizards has been defined based on sand grain size (Stebbins 1944, Norris 1958, Pough 1970,

Turner et al. 1984) and sand compaction (Turner et al. 1984, Barrows 1997). Departures from established thresholds for fringe-toed lizard habitat suitability should correlate with occupancy if habitat quality were a key driver in the observed patterns. Within our study area in the Coachella Valley of southern California, there is a steep precipitation west–east gradient, along the same axis as the distribution of our habitat patches (Barrows & Allen 2007). Coachella Valley fringe-toed lizard population dynamics are driven to a large extent by annual rainfall fluctuations (Barrows 2006). Variation in annual precipitation increases with decreases in mean annual rainfall (Noy-Meir 1973, Bell 1979, MacMahon 1979), so in the more arid eastern valley the lizard populations are more likely to be stressed by stochastic drought events. If the stochastic process hypothesis provides the best model, there should be a strong west–east correlation with persistence and local extinctions.

MATERIALS AND METHODS

Study area. The Indio Hills extend roughly 35 km from the northwest to the southeast, forming a northern boundary to the Coachella Valley, Riverside County, California. The Coachella Valley is situated in the northwestern portion of the Sonoran Desert and is one of the driest and hottest portions of that desert. Annual precipitation varies with a west–east mean annual rainfall gradient of 125 to 79 mm (most recent 60 yr means, Western Regional Climate Center, Palm Springs and Indio reporting stations). The lowest rainfall year occurred in 2002, with from 7 to 4 mm of rainfall recorded across the valley floor. In contrast, in 2005, 326 to 210 mm of rainfall was measured, the largest annual rainfall total recorded in the past 50 yr for some Coachella Valley locations. Temperatures show similar extremes, ranging from a low approaching 0°C in the winter to highs exceeding 45°C commonly recorded during July and August.

Clusters of aeolian sand patches occur throughout the Indio Hills, although most predominantly in the western third, closest to the sand sources (Fig. 1). The sand patches occurred as falling dunes on leeward, east-facing slopes as well as in protected valleys within the Indio Hills. Four discrete sand patch clusters were identified based on potential connectivity within clusters and the lack of likely connectivity between clusters. Barriers to connectivity were identified as locations when the nearest sand patches were separated by rock and coarse alluvium, and when there were no obvious corridors, such as sandy washes or trails, connecting these patches. The closest distance between patch clusters was 1.5 km of rocky substrate. While
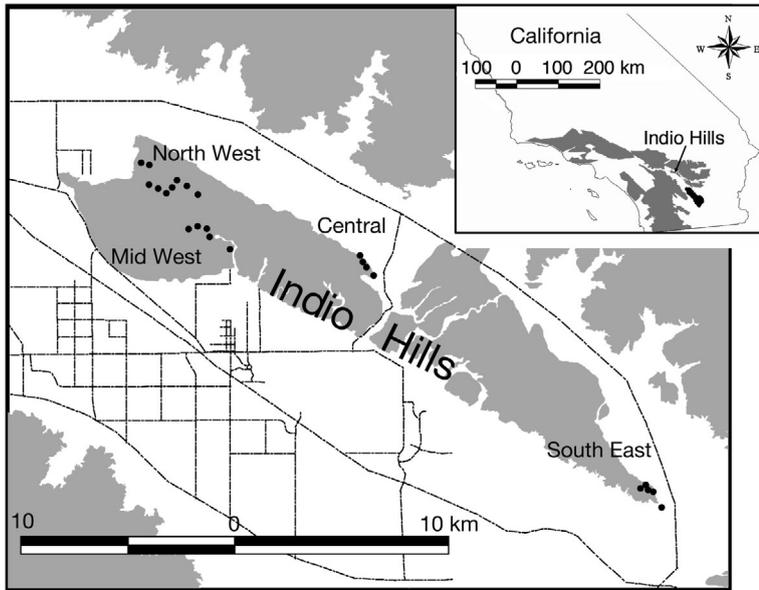
Fig. 1. Distribution of the aeolian sand patches included in the present study. The Indio Hills form a northern border to the Coachella Valley and are located within the northwestern edge of the Sonoran desert in California. Mountain areas are shaded, major roads are shown as lines. Inset shows position of our study area with respect to southern California, USA. North West, Mid West, Central and South East: habitat patches tested

barriers within patch clusters were exclusively the result of geological features, separation of the central and south east sand patch clusters from other clusters was exacerbated by roads, gravel mining, agriculture and suburban development. Centroids for the 4 habitat clusters ranged from 33° 53′ N, 116° 24′ W for the North West cluster, 33° 52′ N, 116° 22′ W for the Mid West cluster, 33° 50′ N, 116°18′ W for the Central cluster, and 33° 45′ N, 116° 10′ W for the South East cluster.

Surveys. Each aeolian sand habitat patch was surveyed 1 to 3 times during April and May in 1993, 2004, 2005, and 2006. Surveys were conducted during the active period for the fringe-toed lizards, when temperatures ranged from ≥35° ≥43°C, measured 1 cm above the sand in full sun, and involved 1 to 2 people repeatedly traversing the habitat patch attempting to flush lizards and identify their diagnostic tracks (Barrows et al. 2006). The steep terrain and fine sand substrate limited the number of sympatric lizard species. The tracks of those lizards that did co-occur with the fringe-toed lizards, such as western whiptails *Aspidoscelis tigris*, and side-blotched lizards *Uta stansburiana*, were distinctive (relative foot size, foot-fall pattern, tail drag or not) and enabled unambiguous identifications. If no fringe-toed lizards or their tracks were located, a patch was re-visited on separate days up to 3 times in a given year. The identification of the lizards' diagnostic tracks enabled surveyors to readily identify lizard occupancy or absence despite the otherwise cryptic and evasive

behaviors used by the lizards. Sighting lizards was always accompanied by observations of numerous diagnostic tracks. Lizards were never found on patches where the tracks were not observed.

Variables. The area and distance between sand patches was measured using ARCVIEW 3.2 software. Sand patch perimeters were digitized from an IKONOS 4 m multi-spectral satellite image taken in 2002. Variables calculated included: the easternmost Universal Transverse Mercator (UTM) (NAD83) coordinate for the center of each sand patch was used to describe the east–west position for each patch; the Distance from each patch to the closest location or patch where there was continuous fringe-toed lizard occupancy during the study duration. Rather than a direct linear distance, the most likely corridor between patches was measured, which often included following sandy washes rather than rocky ridges; Patch Number was the total number of sand patches that appeared to be inter-connected within a patch cluster; and Patch Size was calculated from the digitized perimeter of the sand patch.

Sand compaction has been described as a key habitat variable for Coachella Valley fringe-toed lizards *Uma inornata* (Barrows 1997). For a reference from which to evaluate habitat suitability for fringe-toed lizards on the isolated sand patches, we measured sand compaction and Coachella Valley fringe-toed lizard abundance on 159 belt transects distributed in a stratified random configuration across the aeolian sands of the valley floor (Barrows & Allen 2007). Measures of lizard abundance were based on mean counts of 6 surveys yr^{-1} using diagnostic tracks left in the sand within 100×10 m belts. Sand compaction was measured at 25 points, approximately 4 m apart, along the transect midline, using a hand-held pocket penetrometer with an adapter foot for loose soils (Ben Meadows Company). Due to multiple year measurements at most of these transects, a total of 405 mean sand compaction values were used for the reference data set. Mean sand compaction on sand patches was based on 10+ measurements sand patch^{-1}, collected at points approx. 4 m apart along a randomly located transect across the patch. Sand compaction data were recorded as the force (kg cm^{-2}) required to get the penetrometer 'foot' beneath the sand surface.

Analyses. Logistic regressions were used to evaluate models for explaining the occupancy pattern of lizards on sand patches. The discrete dependent variable was

occupancy, where patches with an occupancy rate of >50% = 1, and those where the occupancy rate was ≤50% = 0. The best models, i.e. those with the lowest AIC (Akaike's Information Criterion) were selected; model ratings were considered distinct when the difference between AIC values was >2.

RESULTS

Occupancy patterns of fringe-toed lizards occurring on the Indio Hills sand patches varied between year and between patch clusters (Table 1). In 1993, 76% of the 26 habitat patches surveyed were occupied by this lizard. Periodic surveys of selected sand patches in each of the 4 patch clusters revealed no changes in occupancy patterns through 1998; however, when the next comprehensive survey of all sites occurred in

2004, occupancy was just 28%. This followed a severe drought in 2002. That year, and for each subsequent year, fringe-toed lizard populations within the Central and South East patch clusters were not detected on any patch and were presumed extinct. The Mid West cluster appears to have stabilized after 2004 with 60% of the patches occupied, and with no re-colonization of either patch G or H. These 2 patches lacked direct connectivity via either sandy washes or trails. The North West cluster maintained the highest occupancy rates throughout the years surveyed, except for 2004 when 44% of the patches were occupied. In each other year when surveys were conducted, 90% of the patches were occupied, although the location of the unoccupied patches varied from year to year.

As an index of habitat suitability for fringe-toed lizards, mean sand compaction for each sand patch was compared throughout their occupied habitat on the valley floor (Fig. 2). Each sand patch considered here had mean compaction values comparable to sites where the lizard populations reach their highest abundances elsewhere (mean sand compaction = 0.08 kg cm^{-2}, SE = 0.009).

Logistic regression analyses were undertaken using variables or variable combinations from Table 1. With just 25 sand patches in the total sample, multivariate analyses were limited to 2 variables to reduce model over-fitting. Although each single and paired variable model provided a statistically significant explanation for the observed occupancy patterns, the low AIC values for both the east–west position of the sand patch (UTM) and the distance to the closest continuously occupied sand patch (Distance) indicated that these 2 variables provided the best single variate models (Table 2). UTM and Distance were correlated with each other (r = 0.937, Pearson pairwise correlation) and are therefore not separate models. The best model for explaining the observed occupancy patterns was a combination of the UTM and Patch Size variables.

At the scale of the entire Indio Hills study area the influence of the east–west gradient dominated the results. To exclude that influence, the logistic regression was repeated for just the western 2 clusters of sand

Table 1. *Uma inornata.* Patterns of occurrence for Coachella fringe-toed lizards. +: occupancy was confirmed; 0: presumed absence. Patch area was calculated from digitized patch perimeters drawn from satellite imagery. Patch distance was the distance to the closest occupied patch (for the lizards). The measurement did not account for topographic barriers and so was likely an underestimate of the true distance a lizard would need to travel between patches

| Habitat patches	Patch size (ha)	Patch distance (m)	*Uma* occupancy 1993	2004	2005	2006
North West						
J	2.73	620	+	+	+	+
K	13.46	620	+	+	+	+
L	1.02	656	+	0	+	+
M	0.41	1484	+	0	+	0
N	4.11	1312	+	0	+	+
O	2.81	514	+	+	+	+
P	0.46	356	+	0	+	+
Q	2.35	514	+	+	+	+
R	0.57	581			+	+
S	0.21	1544	0	0	0	+
Mid West						
A	0.73	624	+	+	+	+
B	1.01	624	+	+	+	+
C	0.42	378	+	+	+	+
G	0.57	589	+	0	0	0
H	0.27	1424	+	0	0	0
Central						
A	1.75	6500	+	0	0	0
B	0.72	6800	0	0	0	0
C	0.06	6900	0	0	0	0
D	0.05	6950	0	0	0	0
E	0.02	6975	0	0	0	0
South East						
A	2.25	15000	+	0	0	0
B	0.39	15000	+	0	0	0
C	0.1	15000	+	0	0	0
G	0.1	15000	+	0	0	0
E	0.1	15000	0	0	0	0
F	0.01	15000	+	0	0	0
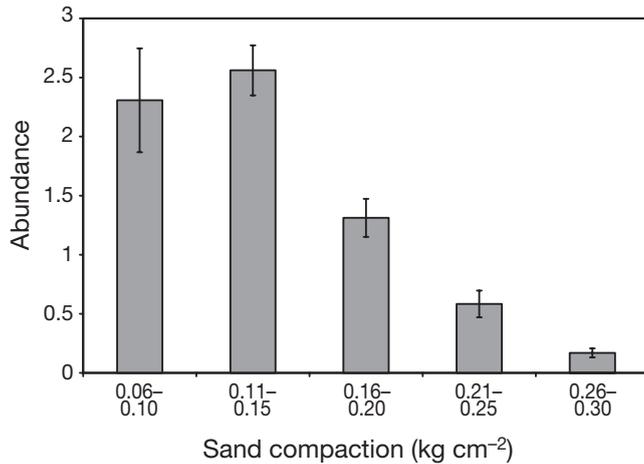
Fig. 2. *Uma inornata*. Patterns of Coachella Valley fringe-toed lizard abundance (mean number of lizards detected on 100 × 1 m belt transects) compared with sand compaction. Error bars indicate 1 SD. Mean sand compaction on the Indio Hills sand patches was 0.08 kg cm^{-2}

Table 2. Results of logistic regression analyses using patch occupancy as the dependent variable (occupancy > 50 % = 1, ≤50 % = 0)

	AIC	Likelihood (χ^2 probability)
ALL SITES		
Single Variables		
UTM	20.74	<0.0001
Distance	22.68	0.0001
Patch #	26.92	0.0011
Patch Size	27.48	0.0014
Paired Variables		
UTM+Patch Size	16.32	<0.0001
Distance+Patch Size	19.74	<0.0001
Distance+Patch #	23.07	0.0002
WESTERN SITES		
Variable(s)		
Patch Size	11.46	0.0023
Patch #	20.26	0.4854
Distance	20.74	0.9308

patches (Table 2). At this more local scale, sand patch size provided the only statistically significant model.

DISCUSSION

A first step in evaluating processes that influence occupancy of isolated habitat patches is to determine the suitability of the habitat within those patches. While for most species this is a difficult task, the primary habitat correlates for Coachella Valley fringe-

toed lizards have been previously defined and described based on sand grain size (Stebbins 1944, Norris 1958, Pough 1970, Turner et al. 1984) and sand compaction (Turner et al. 1984, Barrows 1997). All of the sand patches included in our analyses are aeolian deposits and thus comprise the appropriate sand grain size. Sand compaction measurements confirmed that each site provided habitat characteristics consistent with those sites with high fringe-toed lizard abundance elsewhere on the Coachella Valley floor. High lizard occupancy rates measured in 1993 confirmed that the sand patches provided suitable habitat.

The west–east gradient provided the best single variate logistic model explaining the patterns of fringe-toed lizard occurrence on the sand patches in the Indio Hills; combining that variable with patch size provided the best overall model. Vulnerability to stochastic perturbations, such as drought, increases with small population size; the coupling of these 2 factors therefore fits within existing theory (Wiens 1997). This result is consistent with the hypothesis that stochastic processes, in this case a more severe and prolonged drought in the eastern valley, resulted in patch extinctions.

However, the observed extinction of the central patch cluster had an additional stochastic stressor. The one occupied sand patch there was an actively moving dune. The leading edge moved into an adjacent native California fan palm (*Washingtonia filifera*) oasis, which was hosting a number of predators. American kestrels *Falco sparverius* and loggerhead shrikes *Lanius ludovicianus* used the palm trees as perches to launch their hunting sorties; coupled with the drought effects, the lizards were extirpated at this patch within 1 yr. The same bird species were identified as a leading cause of a 100 to 150 m edge effect, eliminating another lizard species, the flat-tailed horned lizard *Phrynosoma mcallii*, from the boundaries of larger habitat areas on the valley floor (Barrows et al. 2006). Hawlena & Bouskila (2006) found a similar increase in predation on desert lizards and changes in the lizard assemblage resulting from increases in avian predators hunting from planted trees.

To eliminate the influence of the west–east precipitation gradient we conducted a second analysis using only the 2 westernmost sand patch clusters. The results indicated that without that moisture gradient, patch size provided the only statistically significant model to explain patterns of patch occupancy. The importance of patch size in explaining the observed occupancy patterns is an expected result; larger patches should provide habitat for larger lizard populations, which should be more resilient to stochastic processes. However, the sand patches with 100 % occupancy were surprisingly small (mean = 3.5 ha, range 13.46 to 0.42 ha).

Chen et al. (2006) estimated that the minimum habitat patch size for sustaining a Coachella Valley fringe-toed lizard population, if isolated from other populations, was 100 to 200 ha. Only 2 of the 26 sand patches tracked through the duration of our study were sufficiently large to yield a non-negative result when patch area was inserted into their regression model. The area of patches K and N, both occurring in the North West patch cluster, yielded estimated extinction times of 25.5 and 5.7 yr, respectively. Even if we assumed continuous movement between habitat patches within the North West patch cluster, and so combined all patches, the total area was 28.13 ha, yielding an estimated extinction time of 37.9 yr. Exact ages for the isolation of the sand patches were not available; however, given that the most recent aeolian sand movement event into the Indio Hills was in the years immediately following 1937–8 (Griffiths et al. 2002) we assumed a minimum age for all patches of 60 to 70 yr. Aerial photos from 1953 confirm the location and size of each patch conforming to its current configuration over 50 yr ago. Combining the habitat patches within each of the other 3 patch clusters still did not provide sufficient total areas to yield non-negative values. With each sand patch likely having its current level of isolation for over 50 yr, either the Chen et al. (2006) model needs to be reconsidered, or these habitat patches are not truly isolated.

The data used to develop the Chen et al. (2006) model were collected from valley floor sites in the eastern Coachella Valley along with the one occupied sand patch in the Central patch cluster. As our data indicate, stochastic drought has a strong influence on sand patch occupancy in these regions, but a weaker influence in the more mesic western sand patches. Anthropogenically isolated aeolian sand areas on the eastern valley floor have also experienced extinctions, providing support for Chen et al. (2006); however, those in the western valley have not. In addition to the habitat patches included in our analysis we identified 2 additional naturally isolated aeolian sand patches, not in the Indio Hills but in the western valley, with areas less than 13 ha. Both of these sites continue to be occupied with relatively dense fringe-toed lizard populations, yet no similarly sized patches remain occupied in the eastern valley (C. W. Barrows, pers. obs.). The applicability of the Chen et al. (2006) model thus may be limited to truly isolated habitat patches in the eastern Coachella Valley where stochastic processes, especially drought, appear to be the primary drivers of *Uma* population dynamics.

Our data prompt the question as to why, after 60–70 or more years of isolation, the Central and South Eastern sand patch clusters became extinct during our study. In part, the answer may be related to the recent degree of anthropogenic landscape fragmentation that surrounds the Indio Hills. While not necessarily contributing to the extinctions within the clusters, these barriers have permanently restricted the ability for the lizards to recolonize those sites from the remaining *Uma inornata* populations on the valley floor. Another factor explaining the timing of the extinctions is related to the extreme aridity of the central-eastern valley. Variation in annual precipitation increases with decreases in mean annual rainfall (Noy-Meir 1973, Bell 1979, MacMahon 1979). Annual rainfall is a primary driver of Coachella Valley fringe-toed lizard population dynamics (Barrows 2006). The driest year on record for the Coachella Valley was 2002; less than 4 mm fell in the eastern valley that year, and this was preceded and followed by years (1999 through 2004) with below average rainfall. Over the past 75 yr there has been no other continuous 6 yr sequence of below average rainfall (Western Regional Climate Center, Palm Springs and Indio reporting stations). In the eastern valley, 4 of those 6 yr (1999, 2000, 2002, and 2003) experienced rainfall totals less than the 50 mm threshold for positive population growth for Coachella Valley fringe-toed lizards (Barrows 2006). In the western valley conditions were dry as well, but in 2001, 2003 and 2004 rainfall totals all exceeded 50 mm (86 to 117 mm). Predictions of global climate change include both increasing temperatures and a likelihood of decreasing precipitation for this region (Hayhoe et al. 2004). Determining whether the observed precipitation patterns and local extinctions recorded during our study represent the effect and early casualties of global climate change will be a mattter for future retrospective analyses.

Our analyses did not provide support for number of patches or distance to more permanently occupied patches as explanations of our observed pattern of patch occupancy. These variables should have demonstrated some influence if periodic inter-patch movements (an essential component of metapopulation processes) were important there. Despite the lack of statistical support, direct observations of lizards in potential corridors (C. W. Barrows, pers. obs.) indicated that inter-patch connectivity may have a role in structuring the observed occupancy patterns. Those patches that had high occupancy rates on the western patch clusters all had some level of habitat connectivity (dry washes or sandy trails). On the Mid West patch cluster the 2 fringe-toed lizard populations that did become extinct after 1993 (G and H) were not connected to the other 3 occupied patches by sand corridors. Similarly, on the North West patch cluster, patch M had a relatively low occupancy rate and had poor connectivity to the other patches. Although our analyses failed to identify metapopulation dynamics-related

variables as an important patch persistence-extinction process, these direct observations are consistent with a metapopulation hypothesis. Perhaps the stronger influences of drought and patch size overshadowed a weaker metapopulation process, or our variable selection and definition failed to capture the role of connectivity in patch occupancy.

From the perspective of conservation planning, our results indicate that criteria to sustain Coachella Valley fringe-toed lizard populations may differ along the valley's west–east precipitation gradient. In the drier eastern valley larger habitat areas, perhaps as large as Chen et al.'s (2006) 100 to 200 ha estimate, may be required to provide long-term protection for this species. In the western valley, although patch size is important, much smaller minimum areas may be required. Applying the same conservation planning criteria throughout the Coachella Valley could result in not including otherwise sustainable habitats in the western valley, or spending finite conservation funds on non-sustainable lizard populations in the eastern valley.

While these results are specific to a particular site and species, they provide a cautionary tale that has broader implications. Scientists providing guidance to conservation planners need to take care to provide conservation criteria within relevant geographic or situational bounds. Landscapes targeted for conservation are invariably more complex than they first appear. Even in the superficially similar sand dunes of the Coachella Valley, at least 4 distinct communities have been identified, each with unique species associations and population dynamics (Barrows & Allen 2007). Identifying gradients across landscapes and their potential influence on processes that drive persistence and extinction is a critical step in understanding the implications of that complexity to conservation planning.

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