California Fish and Wildlife Special CESA Issue:243-257; 2021

www.doi.org/10.51492/cfwj.cesasi.14

FULL RESEARCH ARTICLE

Forty years later: monitoring and status of the endangered Coachella Valley fringe-toed lizard

CAMERON W. BARROWS[1]* AND SCOTT A. HEACOX[1]

[1] *University of California Riverside, Center for Conservation Biology, Riverside, California, 92521, USA*

**Corresponding Author: cbarrows@ucr.edu*

The Coachella Valley fringe-toed lizard, *Uma inornata*, was listed as endangered under the California Endangered Species Act in 1980. By that time, the lizard's habitat was already reduced by 90%, fragmented into isolated habitat islands on private property among hundreds of landowners. Ecosystem processes that are essential for delivering sand and maintaining the lizard's sand dune habitat were already compromised. As challenging as it was to protect its habitat under these conditions, populations of this lizard still occur across much of the area where it was found forty years ago. Annual monitoring was designed to assess the ongoing viability of these populations by quantifying the effects of potential threats and stressors and focusing adaptive management actions where they are most needed. Here we demonstrate how hypothesis-based monitoring identified specific locations where invasive plant control and sand corridor management were needed to maintain the lizard's populations. By monitoring lizard densities within the context of environmental variables that either drive or inhibit population growth, this monitoring approach informs if, when, and where management actions are needed.

Key words: aeolian sand, California, hypothesis-based monitoring, management intervention, natural versus anthropogenic-driven population fluctuations, nested-scale monitoring, reptile, stressors, *Uma inornata*

The Coachella Valley fringe-toed lizard, *Uma inornata*, (the lizard) (Fig. 1) was listed in 1980 as endangered under the California Endangered Species Act (CESA) and threatened under the federal Endangered Species Act (ESA). Listing a species as endangered requires evidence that habitat loss and/or impacts from other stressors have put that species on a trajectory to extinction. However, the act of listing a species does not alone ensure its protection. The habitat loss and associated stressors that warranted listing need to be managed to halt or reverse population declines. Monitoring informs and assesses the success of ongoing critical management tasks. Here we present a case study underlining the importance of monitoring and management for the protection of the lizard. Now, forty years after those listings, we assess this species' status and the successes and failures of efforts to protect it.

Figure 1. An adult male Coachella Valley fringe-toed lizard, *Uma inornata*. Fringes along the trailing edges of their toes, countersunk lower jaw, overlapping eyelids, and valvular nostrils that keep sand that protect their respiratory tract from breathing in sand particles all provide adaptations for living in an aeolian sand habitat.

The conservation planning and implementation steps for the protection of the lizard have been detailed elsewhere (Barrows 2019). In short, the federal ESA initially took precedence as it offered flexibility under 1982 amendments that allowed the creation of Habitat Conservation Plans (HCPs). HCPs facilitate regional landscape scale conservation planning, not just project by project regulatory requirements for mitigation in response to proposed development impacting endangered species' habitat. Regional planning was an essential and critical task to protect ecosystem processes that transport sand to the lizard's habitat. Since the lizard did not occupy key sand transport corridors, those corridors would not necessarily receive protection under traditional regulatory approaches. With the creation of the Natural Community Conservation Planning Act (NCCP) in 1991, protection efforts for CESA-listed species were given an analogous regional conservation planning approach. The initial single-species HCP for the lizard was signed in 1986 with the fanfare of being the first-ever approved after the 1982 amendments to the ESA. The Coachella Valley Fringe-toed Lizard HCP included multiple municipalities and hundreds of landowners. Being first also meant that there was no template outlining how to proceed and no criteria for defining success or failure.

The lizard's habitat was once a continuous landscape of 33,500 ha of aeolian-sand; however, prior to the 1980 listing and the onset of conservation planning and implementation for this species, the sand dunes had already been reduced by close to 90%, with remaining habitat fragments isolated by roads, freeways, rail corridors, golf courses, agriculture, and suburban developments (Barrows et al. 2008; Fig. 2). A critical concern was that the sand transport corridors were all compromised to one degree or another. A decade after the original lizard HCP was signed it became increasingly clear that the sand corridors were not being adequately protected. Planning began in 1996 to create a federal multiple species HCP (MSHCP) and state NCCP with an explicit ecosystem focus. This effort recognized the need to correct the shortcomings in the original lizard HCP and to extend protection for 27 plant and animal species (including the fringe-toed lizard) and 27 natural communities. Four of the natural communities together encompass the range of aeolian-sand habitats occupied by the lizard: 1) active dunes, 2) stabilized sand fields, 3) ephemeral sand fields, and 4) honey mesquite hummocks and dunes. The state and federal permits for the joint MSHCP/NCCP were signed in 2008.

A monitoring program to assess the degree to which the plan was successful in protecting the lizard and other covered species was developed concurrent with conservation planning efforts. Historically, biological monitoring has focused on periodic counts of a species. Results were limited to determining presence or absence and occupancy trends. However, even healthy populations increase and decrease over time in response to natural fluctuations of limiting resources, predator densities, and other factors. Such natural fluctuations do not necessarily warrant management intervention. Occupancy or abundance data alone do not provide insights as to why changes are happening or what, if any, management prescription might enhance population persistence.

Precipitation is the primary driver of population growth in arid environments (Noy-Meir 1973; Kearney *et al*. 2018). However, the relationship between the lizard's population growth and rainfall is not linear; the seasonality, intensity, and amount of rainfall all have differential effects (Barrows et al. 2009). Monitoring in arid habitats must be able to partition the complex effects of rainfall from other anthropogenic effects to identify if management actions are warranted to reverse population declines. A novel monitoring approach was developed as the MSHCP/NCCP was being negotiated (Barrows et al. 2005; Barrows and Allen 2007a,b). That approach considered monitoring as a series of hypothesis-driven

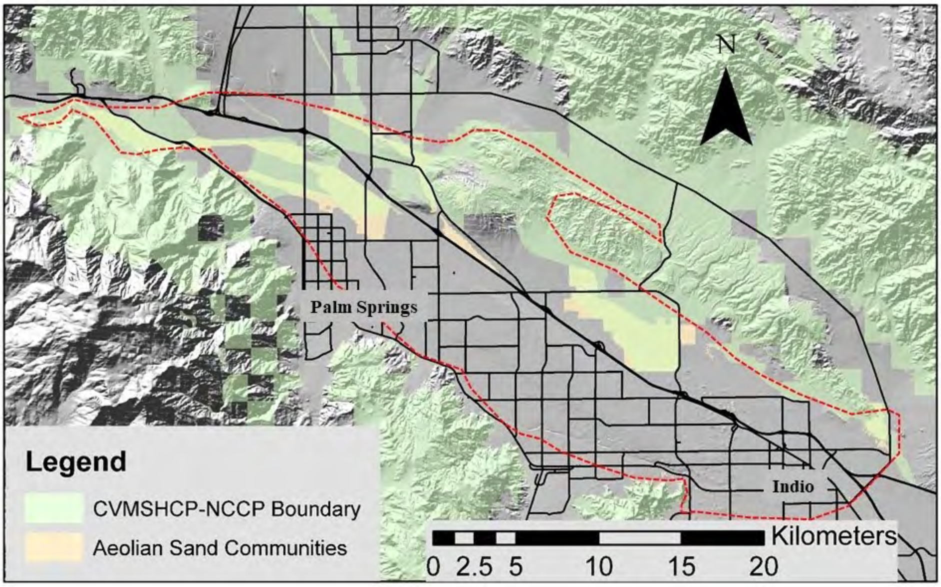

Figure 2. The entire historical range of the Coachella Valley fringe-toed lizard (red-dashed line), as well as remaining aeolian sand habitat, land designated for protection (CVMSHCP-NCCP boundary), and the level of existing fragmentation of those remaining habitats. The aeolian sand habitats shown here are based on US Geologic Survey soil maps but are not precise equivalents to habitat occupied by the lizard. Smaller, isolated habitat fragments and peripheral areas within larger mapped habitat polygons no longer support lizard populations.

experiments using the varying intensity of drivers and stressors over time and space as independent variables, and changes in the lizard's abundance as the dependent, or response variable. Here we present results of monitoring data, employing this hypothesis-driven approach for Coachella Valley fringe-toed lizards covering a 19-year period from 2002–2020.

METHODS

Study Area

The Coachella Valley is located at the northwestern corner of the Colorado Desert, a drier subset of the Sonoran Desert with less influence from summer monsoonal precipitation, broadly stretching west from the Colorado River. This valley is bounded to the west by the Santa Rosa and San Jacinto Mountains, and to the east by the Little San Bernardino Mountains (Fig. 2). The northern boundary of the Coachella Valley is delineated by the southeastern terminus of the San Bernardino Mountains, and the valley extends south to the Salton Sea. The Coachella Valley includes nine incorporated municipalities with a year-round resident population of roughly 400,000 people, from Palm Springs and Desert Hot Springs in the west to Indio and Coachella in the east. However, the number of residents can more than triple during the cooler winter and spring months when seasonal "snowbirds" swell the human population. The regional economy is focused on tourism, second homes, and agriculture.

Habitat conservation efforts are coordinated by the Coachella Valley Conservation Commission (CVCC), a Joint Powers Authority whose members are elected representatives of Coachella Valley cities, indigenous tribes, water districts, and Riverside County. While the lizard's habitat was initially a patchwork of hundreds of privately-owned parcels, current conservation landownership of that habitat includes the U.S. Fish and Wildlife Service National Wildlife Refuges, California Department of Fish and Wildlife Ecological Reserves, U.S. Bureau of Land Management, Coachella Valley Water District, Coachella Valley Association of Governments (CVAG), Coachella Valley Mountains Conservancy (a State of California conservancy), and Friends of the Desert Mountains (a private, non-profit organization). Individual conservation landowners are responsible for land management, while biological monitoring is funded and coordinated by the CVCC. Monitoring protocols are therefore applied evenly across the remaining lizard habitat, independent of land ownership.

Coachella Valley fringe-toed lizards are among six species of the genus *Uma* occupying the Mojave and Colorado Deserts in California, Arizona, and northwestern Mexico (Gottscho et al. 2017; Derycke et al. 2020). Two additional *Uma* species occur in the Chihuahua Desert in north-central Mexico. All species of *Uma* are restricted to or are found at their highest densities on fine, well-sorted, aeolian sand landscapes, with many confined to discrete sand dune systems. Among those eight *Uma* species, two are especially impacted by expanding human development (*U. inornata* and *U. exsul*; García-De La Peña et al. 2015), with the degree of habitat loss and fragmentation most severe for *U. inornata*, the Coachella Valley fringe-toed lizard (Barrows et al. 2008).

Survey Protocol and Dependent Variables

The lizard's sand dune habitat is extremely dynamic. Aeolian sand habitats are continuously shifting down wind, while new upwind sand additions are dependent on stochastic flood events bringing sediments out of the surrounding mountains (Barrows 1996). The aeolian sand habitat includes four different natural community types that comprise the remnants of the original aeolian sand landscape; they are defined by unique wind, sand, and vegetation characteristics (Table 1). Protection goals included maintaining sustaining populations of the lizard within each of these community types. Monitoring goals focused on quantifying lizard densities in response to precipitation, the variation in habitat quality due to aeolian and fluvial sand dynamics, and anthropogenic stressors (Table 2) across each of the four natural communities. We tested and rejected multiple approaches for visual counts of the lizards. Fisher et al. (2020) monitored this species via a mark/recapture approach on a single 2.25 ha plot for +31 years, marking each resident lizard with a unique combination of three colored beads attached to the base of their tails (Fisher and Muth 1989). They were able to acquire both accurate annual population estimates and delineation of home ranges for resident lizards. However, their method was time and effort intensive, typically requiring dozens of surveys per year, and so was impractical to apply to more than one or two plots.

Our solution was to not count the lizards directly, but to quantify lizard densities using their tracks left in the fine aeolian sand. By using tracks, we eliminated the problem of the lizard's variable, inconsistent activity patterns—if any individual was active on a plot during or prior to the survey we could detect it by the diagnostic tracks it left behind. However, determining which species had left tracks, and how many individuals were present introduced challenges. To determine how many lizards were represented by the tracks observed on each transect we used four criteria. First, we only surveyed on mornings after a night with strong enough winds to clear all tracks from the previous day. Second, we followed each set of tracks to determine if it connected with the tracks of a previously counted lizard. Third, we looked for interactions between lizards to determine if we were looking at one or multiple individuals. Fourth, there are considerable size differences between male and female lizards and between juveniles and adults (Barrows and Fisher 2009) and those differences are mirrored in the track widths. Ensuring that the species-track identification was accurate was resolved with adequate training, and when in doubt following the tracks to the lizard that created them. Much like learning to count birds by their calls and songs, accurately identifying tracks is a learnable skill.

A benefit of this method was that we could detect many more lizards, and so could reduce plot size to just 0.1 ha and still have adequate numbers of lizard sightings for robust statistical analyses. With smaller plots and smaller time and effort per plot, we were able to survey 68 core plots (plots resurveyed every year) across the entire range of the lizard, with 4–6 repeated surveys per plot within a six-week survey window. We configured the 0.1 ha plots as 10-m × 100-m rectangles. Those plots were then clustered (3–7 plots) within separate dunes or habitats within the same natural community type, with plot clusters > 500 m apart, (with the exception two clusters that were < 500 m apart as a result of a random placement) from an adjacent plot cluster. Placement of the initial plot within a cluster was random. Thereafter additional plots were either placed randomly or regularly to answer specific questions (such as edge effects). Non-random plot placements occurred within three clusters where we wanted to measure the effect of distance from a road/powerline that formed a habitat edge. Within a cluster we placed plots ≥ 50 m apart to avoid individual lizards overlapping adjacent plots. Fisher et al. (2020) identified home range sizes for females ($\bar{x} = 505\ m^2$) and males ($\bar{x} = 662\ m^2$), which, assuming roughly circular home ranges, equate to home range diameters of 25–29 m, well below the 50-m separation between plots.

Population densities can vary as habitat characteristics vary, and responses to those shifting habitat qualities can become apparent at different scales (Morris 1987; Smith and

Table 1. Characteristics that distinguish the four aeolian sand natural communities found in the Coachella Valley that provide habitat for the Coachella Valley fringe-toed lizard.

Aeolian Community Characteristics	Active Dunes	Stabilized Sand Fields	Ephemeral Sand Fields	Honey Mesquite Dunes
Habitat Area / Number of Habitat Fragments	1370 ha / 5	400 ha / 1	1700 ha / 4	200 ha / 1
Sand	Deep, continuous, well-sorted fine sand with low silt or finer particle content	Well-sorted fine sands form discontinuous shallow layers over compacted layers with higher silt content.	Discontinuous patches of well-sorted fine sands, coarse sands, gravel, rocks, and boulders	Deep, well-sorted fine sand with low silt or finer particle content
Sand Movement	High mobility shifting dunes	Low mobility	Extremely high mobility	Low mobility
Perennial and annual Plant Composition	Sparse perennial and annual cover: *Larrea* sp. and *Atriplex* sp.	Moderate cover of perennials, seasonally high cover of annuals *Larrea* sp. and *Atriplex* sp.	Moderate cover of perennials, sparse annual cover: *Larrea* sp., *Psorothamnus* sp., *Croton* sp., and *Petalonyx* sp.	High cover of mesquite, low to moderate cover of other shrubs: *Prosopis* sp., *Larrea* sp., *Atriplex*, and *Isocoma* sp.
Invasive Plant Species	Low to moderate cover of *Brassica* sp.	Moderate to high cover of *Brassica* sp. and *Schismus* sp.	Low to zero cover of invasive species	Moderate cover of *Brassica* sp. and *Schismus* sp.

Ballinger 2001). Collecting lizard densities at a plot scale (0.1 ha) that can be combined and analyzed as plot clusters provides analytic flexibility at multiple scales. Plot clusters can be combined at the natural community or landscape scale. Our 68 core plots included replicates within the four natural communities as follows (plot clusters/total # of plots): active dunes (4/18); mesquite dunes (1/11); ephemeral sand fields (3/18); and stabilized sand fields (3/21).

Two to three people surveyed each plot: a professional biologist plus 1–2 volunteer community scientists. Surveyors slowly walked equidistant from each other along the length of the plot, noting and identifying all vertebrate tracks, which were then verified and recorded by the biologist. The addition of the community scientists significantly increased detection rates for lizards and their tracks (Barrows et al. 2016).

While population density is a useful metric, it is dependent on long-term habitat conditions. It can take multiple years for a population to substantially increase density due to the finite number of breeding adults. Similarly, it can take years for densities to decline due to multiple-year lifespans. Population growth rate (γ) can prove to be a more sensitive response variable to shorter term changes in independent variables. Here population growth was calculated as $\gamma = \ln(N_{i+1}/N_i)$, where N_i is the population density in year $_i$, and N_{i+1} is the population density the following year.

Table 2. Primary stressors impacting the Coachella Valley fringe-toed lizard, their effects, and management responses for reducing those impacts.

Stressor	Scale	Effect	Management Response
Climate Change	Broad, but most severe at the eastern, hotter/drier conserved habitats	Reduced surface activity for the lizards, more severe droughts, reduced vegetation cover. Higher mortality and lower recruitment rates	Reduce impacts from other stressors
Invasive Plant Species	Localized, varies between sites, and between species. Most severe where there are lower sand transport rates	Sand stabilization, outcompetes native annuals, reducing both plant and insect food resources for the lizards. Notably, insect abundance and diversity are reduced as Sahara mustard increases	Hand removal is the safest, but the scale of the infestations easily overwhelms staff or volunteers for large scale removal efforts. Removal efforts then need to be strategically targeted to the habitats with the greatest benefits
Edge Effects	Localized	Increased predation from greater roadrunners, American kestrels, and common ravens	Remove anthropogenic nesting sites and power lines used as perches by predators
Loss of Genetic Heterogeneity	Broad, but most severe on the smallest habitat patches	Potential reduced adaptability to climate change and other stressors. Otherwise unexplained population declines	Translocation of gravid females and/or hatchlings to increase heterogeneity. Adults do not appear to translocate as successfully.
Loss of Ecosystem Processes	Localized	Increased sand stabilization, reduced active, loose sand habitats	Keep sand corridors open. Recycle fugitive sand (sand on roads or otherwise unwanted areas) to sand corridors
Off-road Vehicle Trespass	Localized	Reduced perennial vegetation cover. Increased debris dumping	Maintain fencing, increased law enforcement patrols

Independent Variables

Although this region receives occasional isolated summer rain that can result in localized flooding, primary productivity and breeding success of the lizards is usually catalyzed by cool season rains (Noy-Meir 1973; Kearney *et al.* 2018). To illustrate the relationship between rainfall and the lizards' population dynamics we compared annual November-April rainfall totals from the eastern-most protected habitat, the Coachella Valley National Wildlife Refuge and California State Ecological Reserve. Rainfall data were collected on site and were found to be nearly identical to a nearby, internet accessible weather station in the city of Indio (https://wrcc.dri.edu/cgi-bin/cliMAIN.pl?ca4259). Rainfall levels do vary across the Coachella Valley, with an increase toward the western edge of the valley at the western limits of the lizards' remaining habitat; however, the relative trajectories (drought, average rainfall, or relatively wet conditions) are consistent throughout the region. Using this rainfall metric to illustrate relationships between rainfall and lizard population dynamics throughout the lizards' range, while not precise for specific locations, provides the opportunity to assess how drought or wetter conditions influence the lizards' population densities. Rainfall levels provide a coarse-scale expectation of population growth rate trajectories.

Additional independent data that we collected annually on each 0.1 ha plot included: 1) spring annual and perennial plant abundance and density by species, including both native and non-native species; 2) arthropod abundance and species diversity, 3) sand compaction, and 4) associated vertebrates, using track counts collected at the same time that the lizards were surveyed. These metrics provided fine-scale, plot-specific indicators of habitat characteristics. For annual vegetation cover we measured both and density and percent cover by species, on 12, 1-m^2 sub-plots, four at each end and one in the center of each 0.1 ha plot. We measured arthropods using three pitfall traps placed overnight, one at each end and one in the center of each 0.1 ha plot. One of those arthropods, the beetle *Asbolus* (previously *Cryptoglossa*) *laevis*, (Tenebrionidae) proved to be a useful indicator of sand compaction, only occurring on the less compacted sands of active dunes (Barrows 2000). Sand compaction was measured using a Pocket Penetrometer (AMS Inc.). Twenty-five compaction measurements, each separated by roughly 4 m, were made along the mid-line of each plot. We measured associated vertebrates using the same track protocol used to measure the lizard densities. Some of the associated vertebrates are predators and so could influence fringe-toed lizard abundance. Potential predators include leopard lizards (*Gambelia wislenzenii*), sidewinders (*Crotalus cerastes*), coachwhips (*Masticophis flagellum*), glossy snakes (*Arizona elegans*), greater roadrunners (*Geococcyx californianus*), loggerheaded shrikes (*Lanius ludovicianus*), common ravens (*Corvus corax*), American kestrels (*Falco sparverius*), coyotes (*Canis latrans*), and potentially some species of rodents (Timberlake and Washburne 1989). Others are possible competitors such as zebra-tailed lizards (*Callisaurus draconoides*) and flat-tailed horned lizards (*Phrynosoma mcallii*), but none are as habitat specific to active aeolian sand as are fringe-toed lizards.

RESULTS

Figure 3 illustrates the nested-scale character of the fringe-toed lizard monitoring data. At the finest scale (Fig. 3a) are individual plots clustered within a single active dune (AD2). Means for the combined plots within each of the four individual active dune plot clusters (replicates within the active dune natural community) are shown in Figure 3b (middle scale). Finally, at the coarsest scale (Fig. 3c) are the combined means for each of the four natural communities across the lizards' entire range. At each of these scales the data can reveal patterns that provide insights regarding the status of the lizard. At both the fine-scale plot level for the AD2/active dune cluster (Fig. 3a) and the combined active dune natural community (Fig. 3b) scale, precipitation levels positively correlate with lizard densities (Pearson's Correlation: AD2 plot cluster: df = 17, r = 0.717, P = 0.0008; all active dune communities: df = 17, r = 0.581, P = 0.011). At the coarsest natural community scale (Fig. 3c), the correlation (r) between lizard density and precipitation was uneven. The strongest correlation was with active dunes. Next was the mesquite dunes (df = 17, r = 0.514, P = 0.029), followed by non-significant rainfall-lizard density correlations for stabilized sand fields (df = 17, r = 0.317, P = 0.199), and ephemeral sand fields (df = 14, r = 0.077, P = 0.785).

Since the plots are replicate surveys within each dune, and the dunes are replicates within the natural community, the general within year synchrony provides validation for

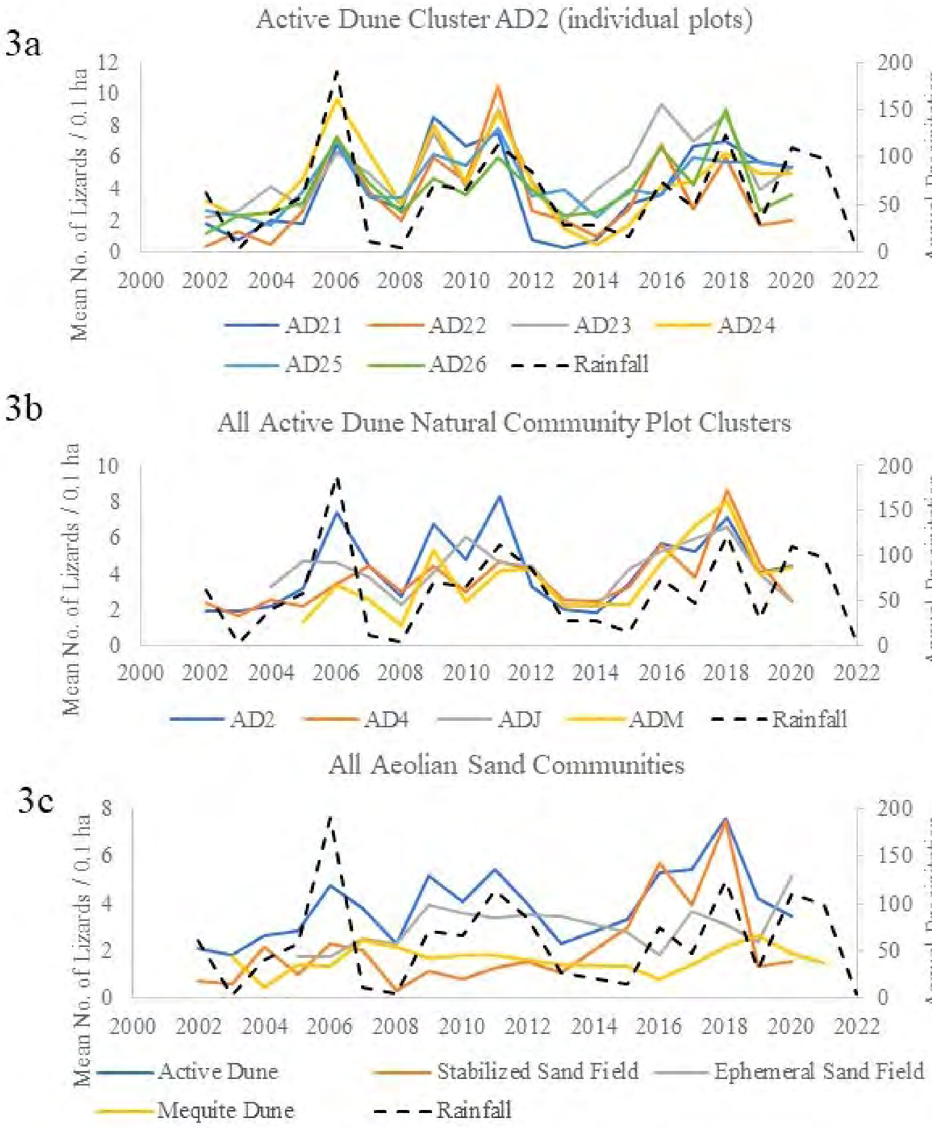

Figure 3. Annual changes in lizard density at multiple scales within the context of precipitation to show how the lizards' population fluctuations are often synchronized with rainfall patterns. Since lizard density is in part a reflection of the previous year's reproductive recruitment, precipitation is shifted back by one year so that lizard density aligns with the precipitation effects.

the ability of the plot size and survey methodology to detect real change when it happens. Large population swings are a regular occurrence and should not influence management responses if they are synchronized in direction and amplitude with shifting rainfall levels. The question then is when does asynchronous, or non-significant correlations between precipitation and lizard densities indicate a need for management intervention?

A list of potential stressors that could warrant management responses is shown in Table 2. Of those that have localized impacts, off-road vehicles could be discounted as no recent vehicle trespasses were observed. Invasive species impacts and losses of ecosystem processes (reduced sand delivery) can be interrelated and so are difficult to partition. However, looking at that middle scale graph, in 2020 there were opposite population trajectories for the AD2 and ADM plot clusters (increasing) versus the AD4 and ADJ clusters (decreasing). Those divergent trajectories warranted further analyses. The AD2 and ADM plot clusters did have significantly less Sahara mustard, *Brassica tournefortii*, than the AD4 and ADJ sites (Means 13.23 versus 24.75 plants/m^2; ANOVA df = 1, F = 4.5313, P = 0.049), and had a significantly higher (and positive) population growth rate (means $\gamma = 0.103$ versus -0.644; ANOVA df = 1, F = 18.9855, P = 0.00049). While densities AD2 and ADM were less than that for the Ephemeral Sand Field natural community (Fig. 1), a habitat that lacked Sahara mustard, their respective population growth rates were not significantly different (means $\gamma =$ 0.103 versus 0.57; ANOVA df = 1, F = 4.0887, P = 0.0561). The mustard densities on AD4 and ADJ appear to have exceeded a tipping point for negatively impacting the lizards. An illustration of the varying Sahara mustard densities that can occur across the active dunes and stabilized sand fields are shown in Figure 4.

The regression of 2020 lizard density versus sand compaction was significant for both active dunes ($R^2 = 0.5939$; $P < 0.00001$) and stabilized sand fields ($R^2 = 0.2101$; $P < 0.003$); less compacted sand in correlated with higher densities of fringe-toed lizards (Fig. 5). There appears to be a sand compaction level of approximately 0.125 kg / cm^2 that distinguishes most active dunes from stabilized sand fields. Of the AD2 and ADM plots designated *a priori* as active dunes, 75% had sand compaction levels fitting to that natural community. However, for the AD4 and ADJ active dune plots, just 30% had sand compaction levels $\leq$ 0.125 kg / cm^2. The occurrence of plots previously identified as active dunes, but now with sand compaction and lizard densities well within the stabilized sand field range, identified a need to initiate remedial management. Although roadrunner, kestrel, and raven densities increased with proximity to human development, we did not find any support for other additional explanations, such as edge effects which are manifested by increases in potentially anthropogenically augmented predator densities (i.e., roadrunners, ravens, or kestrels). However, both the roadrunner (except on the mesquite dune natural community) and kestrel were dependent on planted non-native trees and shrubs for nesting sites. Our data identified that management intervention to remove mustard as well as remove any other barriers to aeolian sand movement was warranted on the AD4 and ADJ dunes. The lack of synchrony between lizard density and coarse scale precipitation data identified that a potential problem existed; finer scale invasive species densities and sand compaction data identified the cause and management solutions.

DISCUSSION

Wild populations fluctuate naturally in size from year to year. The challenge for managing endangered species that are facing multiple stressors is distinguishing natural population

Figure 4. The top image shows the infestation of Sahara mustard (the dense, straw colored plants) on an active dune (AD2) during the wet spring of 2005. The lower image shows the density of mustard on an adjacent stabilized sand field that same year.

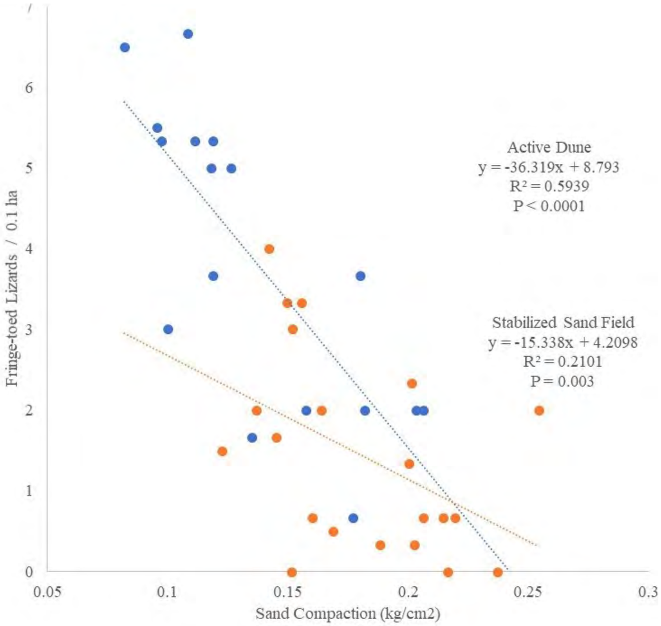

Figure 5. Patterns of Fringe-toed lizard densities in relationship to sand compaction in 2020. Active dunes (each plot indicated by a blue circle) generally have less compacted sand and higher lizard densities, whereas stabilized sand field plots (orange circles) have more compacted sand and fewer lizards. The regression of lizard density versus sand compaction for each habitat type show statistically significant correlations. The plots identified as active dunes, but that have values that are well within those for stabilized sand fields are not receiving new sand and are being invaded by Sahara mustard.

oscillations from population shifts that are anthropogenic driven that, if not managed, could result in population declines leading to extinction. Here we provided examples of how the hypothesis-driven monitoring approach employed for the Coachella Valley fringe-toed lizard has clarified those distinctions and identified site-specific management recommendations. Using two abiotic metrics, precipitation (coarse scale) and sand compaction (fine scale), plus a biotic metric (invasive plant densities), we identified site-specific priorities for managing an invasive weed, Sahara mustard, to promote more sustainable lizard populations. Without management intervention, some active dune communities, habitats that where the lizard populations are consistently the densest throughout its range, appear to be transitioning to stabilized sand fields, a natural community with consistently the lowest lizard densities.

We continue to find that increasing mustard density decreases native plant abundance (Barrows et al. 2009), decreases arthropod abundance (Hulton et al. 2013), and increases sand compaction. As Sahara mustard density increased, lizards became increasingly scarce, and ultimately absent. Our findings indicate that the mustard continues to be a significant threat to the sustainability of the lizard populations, especially on stabilized sand fields and active dunes. This is in contrast to our findings that another invasive weed, Russian thistle, *Salsola tragus,* had a benign to positive impact on the lizards (Barrows 1997).

The density of mustard is tied to both the amount of rainfall and sand transport rates - the more rainfall and the more stable the sand, the denser the mustard. Mustard density is influenced by both the amount of rainfall and the timing of rainfall. Heavy early December rains guarantee a dense growth of mustard, but if the rains do not start until late February or March, little mustard germinates (Barrows et al. 2009). If there is a sequence of storms beginning in December and continuing through February, a new cohort of mustard germinates after each storm. These patterns complicate control efforts. Herbicides that kill mustard will also kill native annual plant species, and mustard will still germinate following an herbicide treatment if more storms occur. Accordingly, "surgical" hand pulling, focusing on areas where mustard removal will yield the greatest benefits, is the preferred control method. Unless a safe, species-specific biological control for the mustard is identified, hand pulling will be an ongoing management task.

Stabilized sand fields did not have significant correlations with precipitation. Stabilized sand fields have the highest levels of Sahara mustard infestation as well as the highest sand compaction levels of any of the aeolian sand communities. *Asbolis laevis* beetles were not detected in this dune type, and fringe-toed lizards only rarely exceeded a mean of 2 lizards/plot (Figs. 3, 5).

Ephemeral sand fields also did not have significant correlations with precipitation; this community occurs in a region of the Coachella Valley where wind and sand transport are so strong as to continue to blow deposited sand downwind and scour rocks into ventifacts (Table 1). Within the ephemeral sand fields, due to these strong winds, sand residence time is relatively short compared to the other aeolian sand-based natural communities. These scouring winds also inhibit annual plant growth (including non-native invasive species), so higher annual rainfall that supports annual plant growth and arthropod prey for the lizards elsewhere has less of an impact on the lizard's population dynamics here, and a close correlation between annual precipitation and the lizard's population growth is not expected. Rather, when sand delivery is sufficient to build sand hummocks, and when that coincides with sequential years of average or greater rainfall to maintain high soil moisture to support leaf and flower production of perennial shrubs, the lizard population grows, as it did in 2020. Understanding site-specific interactions between abiotic inputs and biotic responses is critical for developing models from which the need for management interventions can be determined. For this natural community there are up-wind sand corridor challenges, such as sand and gravel mining, channelization for aquifer re-charging, and conflicts associated with roadways that cross the sand corridor. Each of these could restrict sand delivery to this habitat, and each needs to be monitored to ensure sand delivery is not constrained.

We have previously addressed questions that included whether the high degree of habitat fragmentation had resulted in a loss of genetic diversity in the lizards. Based on tissue samples collected in the mid-1990s, Hedtke et al. (2007) found no genetic structure associated with the lizard populations occupying the different fragments; their genetic profile reflected the pre-fragmentation, panmictic condition. A follow-up study analyzing tissues collected in 2008, (Vandergast et al. 2016) found a different result; lizard populations occupying each habitat fragment had a unique genetic signature, and each population had lost genetic diversity relative to that 1990s baseline. Climate change also looms as a threat to the lizards. Barrows et al. (2010) modeled the response of the fringe-toed lizards to expected levels of climate change if no significant reductions in anthropogenic greenhouse gases occur and found that only the westernmost habitat areas will likely continue to provide the climate envelope currently preferred by the lizards. For the present, we found lizards are sustaining populations as expected with respect to annual rainfall and Sahara mustard densities in all the remaining protected habitats. Given that land managers do not have the capacity to alter the course of climate change, it is imperative that they address those threats that they can affect. These include controlling invasive plants and keeping sand corridors unobstructed, and reducing other stressors that might, together with climate change, result in local extirpations.

Forty years after the listing of the Coachella Valley fringe-toed lizard as endangered, this species continues to occupy much of the same landscape they occupied in 1980. Land protection efforts, purchasing essential private parcels and so taking them out of a trajectory toward future development, has been extremely successful. However, long-term success, defined as maintaining sustaining fringe-toed lizard populations across those protected lands, will depend on effective management informed by hypothesis-based monitoring.

ACKNOWLEDGEMENTS

We want to express our gratitude to volunteer community scientists, agency partners, and staff who have helped facilitate and conduct our lizard and habitat monitoring efforts. They include Tracy Bartlett, Jennifer Chiu, Melanie Davis, John Frazier, Larry Heronema, Sara Miller, Paisley Ramstead, Matthew Salkiewicz, Christian Schoneman, Peter Schwartz, Razia Shafique-Sabir, Sue Shigenaga, Lloyd Shigenaga, Lynn Sweet, Alicia Thomas, Gary Ward, and Cathy Wiley. Katherine Barrows and four anonymous reviewers provided edits which improved our manuscript tremendously.

LITERATURE CITED

Barrows, C. W. 1996. An ecological model for the protection of a dune ecosystem. Conservation Biology 10:888–891.

Barrows, C. W. 1997. Habitat relationships of the Coachella Valley fringe-toed lizard, *Uma inornata*. Southwestern Naturalist 42:218–223.

Barrows, C. W. 2000. Tenebrionid species richness and distribution in the Coachella Valley sand dunes (Coleoptera: Tenebrionidae). Southwestern Naturalist 45:306–312.

Barrows, C. W. 2019. The Coachella Valley solution: balancing economic development and the protection of a threatened lizard. Chapter 6 in O.P. Perkins, editor. Advances in Animal Science and Zoology, Volume 14. Nova Science Publishers, Hauppauge, NY, USA.

Barrows, C. W., E. B. Allen, M. L. Brooks, and M. F. Allen. 2009. Effects of an invasive plant on a desert sand dune landscape. Biological Invasions 11:673–686.

Barrows, C. W., and M. F. Allen. 2007a. Biological monitoring and bridging the gap between land management and science. Natural Areas Journal 27:194–197.

Barrows, C. W., and M. F. Allen. 2007b. Community complexity: stratifying monitoring schemes within a desert sand dune landscape. Journal of Arid Environments 69:315–330.

Barrows, C. W., and M. Fisher. 2009. Coachella fringe-toed Lizard. Pages 266-269 in L. C. Jones and R. E. Lovich, editors. Lizards of the American Southwest. Rio Nuevo Publishers, Tucson, AZ, USA.

Barrows, C. W., J. Hoines, M. S. Vamstad, M. L Murphy-Mariscal, K. Lalumiere, and J. Heintz, 2016. Measuring the value of citizen scientists for assessing climate change impacts across desert ecoregions. Biological Conservation 195:82–88

Barrows, C. W., K. L. Preston, J. T. Rotenberry, and M. F. Allen. 2008. Using occurrence records to model historic distributions and estimate habitat losses for two psammophilic lizards. Biological Conservation 141:1885–1893.

Barrows, C. W., J. T. Rotenberry, and M. F. Allen. 2010. Assessing sensitivity to climate change and drought variability of a sand dune endemic lizard. Biological Conservation 143:731–743.

Barrows, C. W., M. B. Swartz, W. L. Hodges, M. F. Allen, J. T. Rotenberry, B. Li, T. A. Scott, and X. Chen. 2005. A framework for monitoring multiple species conservation plans. Journal of Wildlife Management 69:1333–1345.

Derycke, E. G., A. D. Gottscho, D. G. Mulcahy, and K. de Queiroz. 2020. A new cryptic species of fringe-toed lizards from southwestern Arizona with a revised taxonomy of the *Uma notata* species complex (Squamata: Phrynosomatidae). Zootaxa 4778:67–100.

Fisher, M., and A. Muth. 1989. A technique for permanently marking lizards Herpetological Review 20:45–46

Fisher, M., A. Muth, and R. F. Johnson. 2020. A long-term study of home range of Coachella fringe-toed lizards, *Uma inornata*. Journal of Herpetology 54:174–182.

García-De La Peña, C., C. W. Barrows, H. Gadsden, M. Fisher, G. Castañeda, and U. Romero-Méndez. 2015. Conservation challenges in Mexico: developing a protection strategy for the threatened sand dunes of Coahuila's La Laguna. Pages 81-97 in J. Galindo, editor. Mexico in Focus: Political, Environmental and Social Issues. Nova Science Publishers, Inc. Hauppauge, NY, USA.

Gottscho, A. D., D. A. Wood, A. G. Vandergast, J. Lemos-Espinale, J. Gatesy, and T. W. Reeder. 2017. Lineage diversification of fringe-toed lizards (Phrynosomatidae: *Uma notata* complex) in the Colorado Desert: delimiting species in the presence of gene flow. Molecular Phylogenetics and Evolution 106:103–117.

Hedtke, S. M., K. R. Zamudio, C. A. Phillips, J. Losos, and P. Brylski. 2007. Conservation genetics of the endangered Coachella Valley fringe-toed lizard (*Uma inornata*). Herpetologica 63:411–420.

Hulton, H. L., A. M. Hansen, C. W. Barrows, Q. Latif, M. W. Simon, and K. E. Anderson. 2013. Shifts in arthropod community structure during an invasion of desert ecosystems by Sahara mustard (*Brassica tournefortii*). Biological Invasions 16:1675–1687.

Kearney, M. R., S. L. Munns, D. Moore, M. Malishev, and C. M. Bull. 2018. Field tests of a general ectotherm niche model show how water can limit lizard activity and distribution. Ecological Monographs 88:672–693.

Morris, D. W. 1987. Ecological scale and habitat use. Ecology 68:362–369.

Noy-Meir, I. 1973. Desert ecosystems: environment and producers. Annual Review of Ecology and Systematics 4:25–51.

Smith, G. R., and R. E. Ballinger. 2001. The ecological consequences of habitat and microhabitat use in lizards: a review. Contemporary Herpetology 2001(3):1–28

Vandergast, A. G., D. A. Wood, A. R. Thompson, M. Fisher, C. W. Barrows, and T. J. Grant. 2016. Drifting to oblivion? Rapid genetic differentiation in an endangered lizard following habitat fragmentation and drought. Diversity and Distributions 22:344–357.

Submitted 19 August 2020
Accepted 30 September 2020
Associated Editor was D. Applebee