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POPULATION DYNAMICS OF A THREATENED SAND DUNE LIZARD

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Abstract—Understanding how and why the abundance of a species changes in space and time is an essential component to effective endangered species conservation. Key to this understanding is being able to distinguish natural population dynamics from a downward trajectory of a species at risk of extinction. For many species in arid environments, rainfall drives population changes. This is the case for Coachella Valley fringe-toed lizards (*Uma inornata*), a species listed as threatened under the U.S. Endangered Species Act. At low rainfall levels, the lizards exhibit negative population growth until annual precipitation exceeds 40 to 50 mm. Fluctuation in the population growth of the lizards is also correlated with changes in their diet. A regression model using rainfall and diet to explain lizard population dynamics resulted in a significant R^2 value of 0.956. Because drought is common in their arid environment, it is not unusual for this lizard species to endure consecutive years of population declines. Fringe-toed lizard population counts during extended droughts often approach zero, yet the populations quickly rebound during periods of near average rainfall. If counts approaching zero are not reliable thresholds for when remedial management actions are warranted, then monitoring based management decisions need to use criteria that are more heuristic. Departures from the rainfall-diet-population growth model might provide the signal needed for management actions.

Resumen—El entendimiento de cómo y porqué la abundancia de especies cambia en espacio y tiempo es un componente esencial para la efectiva conservación de especies en peligro de extinción. La clave para dicho entendimiento es poder distinguir entre la dinámica natural de las poblaciones y la trayectoria descendiente de una especie en riesgo de extinción. Para muchas especies en ambientes áridos, las lluvias conducen a cambios poblacionales. Este es el caso para la lagartija del Valle de Coachella (*Uma inornata*), especie listada como amenazada dentro del Acta de Especies en Peligro de Extinción de USA. Las lagartijas en niveles bajos de lluvia muestran un crecimiento poblacional negativo hasta que la precipitación anual excede 40–50 mm. Las fluctuaciones en el crecimiento poblacional de las lagartijas están también correlacionadas con los cambios en su dieta. Un modelo de regresión utilizando lluvias y dieta para explicar la dinámica poblacional de las lagartijas resultó en un R^2 significativo de 0.956. Debido a que la sequía es común en su ambiente árido, no es inusual para esta especie de lagartija el soportar consecutivamente declinación en las poblaciones a través de los años. Los conteos poblacionales de *Uma inornata* durante sequías extensas usualmente se acercan a cero, sin embargo las poblaciones se reponen rápidamente durante periodos cercanos al promedio de precipitación. Si los conteos que resultan en cero no son confiables para justificar el manejo correctivo, entonces las decisiones de manejo basadas en el monitoreo necesitan usar un criterio más heurístico. Desviaciones del modelo de crecimiento poblacional con lluvias y dieta pueden proveer de información necesaria para acciones de conservación.

Natural population fluctuations are common in species (Pechmann et al., 1991, Blaustein et al., 1994) and are generally no cause for alarm. However, not all declines are natural (Gibbons et al., 2000). Distinguishing between natural population dynamics versus a downward trajectory of a population at risk of extinction becomes a critical challenge for insuring the conservation of endangered species (Pechmann et al., 1991). Barrows et al. (2005) proposed a conceptual framework for addressing this key problem. Central to that framework is an understanding of what environmental factors drive the abundance of a species over space and time. This understanding is particularly acute in isolated, fragmented habitats that lack the buffering effects of connectivity to larger populations.

Here I provide an analysis of 20 years of data on population drivers for isolated populations of the Coachella Valley fringe-toed lizard, *Uma inornata*, a species listed as threatened under the U. S. Endangered Species Act. Historically, desert sand dunes systems, the sole habitat for this species (Stebbins, 1944; Norris, 1958; Barrows, 1997), stretched across much of the floor of the Coachella Valley in the Colorado Desert of southern California, providing nearly continuous 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 a 95% loss of this habitat (Barrows, 1996) and severely fragmented remaining viable habitat. Implementation of a regional conservation initiative aimed at finding an adequate balance between species protection and continued economic development, termed a habitat conservation plan, was begun in 1986. The habitat conservation plan requires that monitoring occur to assess the status of the fringe-toed lizard populations. Population estimates alone rarely provide sufficient information to identify thresholds for when or how an adaptive management regime (Holling, 1978; Walters, 1986) should be employed for a species that is the focus of a conservation effort (Barrows et al., 2005). My objective was to identify one such threshold, using an analysis of the population dynamics of *U. inornata* and correlations between annual rainfall and food resources to generate a predictive model to track and forecast natural population oscillations. Departures from natural population fluctuations predicted by such a model could signal a need for remedial management actions.

In arid ecosystems, highly variable and unpredictable precipitation often becomes the driver of biological processes (Noy-Meir, 1973). Support for this axiom can be found across a broad range of taxa and regions (Mayhew, 1965, 1966; Pianka, 1970; Ballinger, 1977; Whitford and Creusere, 1977; Seely and Louw, 1980; Dunham, 1981; Abts, 1987; Robinson, 1990; Brown and Ernest, 2002; Castañeda-Gaytán et al., 2003; Germano and Williams, 2005). Climatic effects can be particularly acute in extremely arid deserts as variation in annual precipitation increases with decreases in mean annual rainfall (Noy-Meir, 1973; Bell, 1979; MacMahon, 1979).

Maximizing reproductive success during periods of high resource abundance can be critical for sustaining population viability through extended droughts. For desert lizards, higher reproductive success often correlates with increased rainfall (Robinson, 1990). This might be due to increased food availability from annual plant growth and phytophagous insects (Pianka, 1970; Ballinger, 1977; Ballinger and Ballinger, 1979; Seely and Louw, 1980; Dunham, 1981; Robinson, 1987, 1990). This pattern should have the strongest correlation with longer-lived species, which can forego breeding except when environmental conditions might result in higher reproductive success (Williams, 1966; Tinkle, 1969).

METHODS—*Study Area*—Data were collected on 3 active sand dunes within the Thousand Palms Preserve in the Coachella Valley near Palm Springs, Riverside County, California. Historically the valley soils were overlain with extensive sand dunes arising from flood outwash events from the San Bernardino Mountains to the northwest, San Jacinto Mountains to the southwest, and the Little San Bernardino Mountains (Joshua Tree National Park) and Indio Hills to the north. The Coachella Valley is classified as an extremely arid (Noy-Meir, 1973) shrub desert with a mean annual rainfall of 79 to 125 mm (most recent 60-year means, Western Regional Climate Center, Palm Springs and Indio reporting stations). The lowest rainfall year occurred in 2002, with just 4 to 7 mm recorded across the valley floor. 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.

The Thousand Palms Preserve is in the central Coachella Valley and has a 60-year average precipitation of 79 mm. Aeolian sand at Thousand Palms Preserve is finer than in dune habitats farther west and forms active sand fields and dunes that are migrating over a fine silt substrate. Two plots (TPP1 and TPP2) were located approximately 2 km apart (33°47′N, 116°20′W) on separate active dunes, each >50 ha, with sparse perennial vegetation dominated by creosote bush (*Larrea tridentata*) and saltbush species (*Atriplex canescens* and *A. polycarpa*). While these dunes were separated in terms of their physical location, there was likely biological connectivity between them. The interdune habitat consisted of an aeolian sand hummock habitat where fringe-toed lizards also occurred, although in much lower densities. Data were collected from 1986 to 2005 (TPP1) and from 1990 to 2005 (TPP2). A third plot (TPP3) was established on a physically and biologically isolated dune (33°51′N, 116°19′W) approximately 1 ha in size, 6 km north of TPP1 and TPP2. The habitat on this site differed from TPP1 and TPP2 in that it was adjacent to a natural desert fan palm (*Washingtonia filifera*) oasis and included phreatophytic vegetation, such as honey mesquite (*Prosopis glandulosa* var. *torreyana*) and arrowweed (*Pluchea sericea*). Data were collected at TPP3 from 1996 to 2000, after which fringe-toed lizards were extinct on this site (Chen et al., 2006).

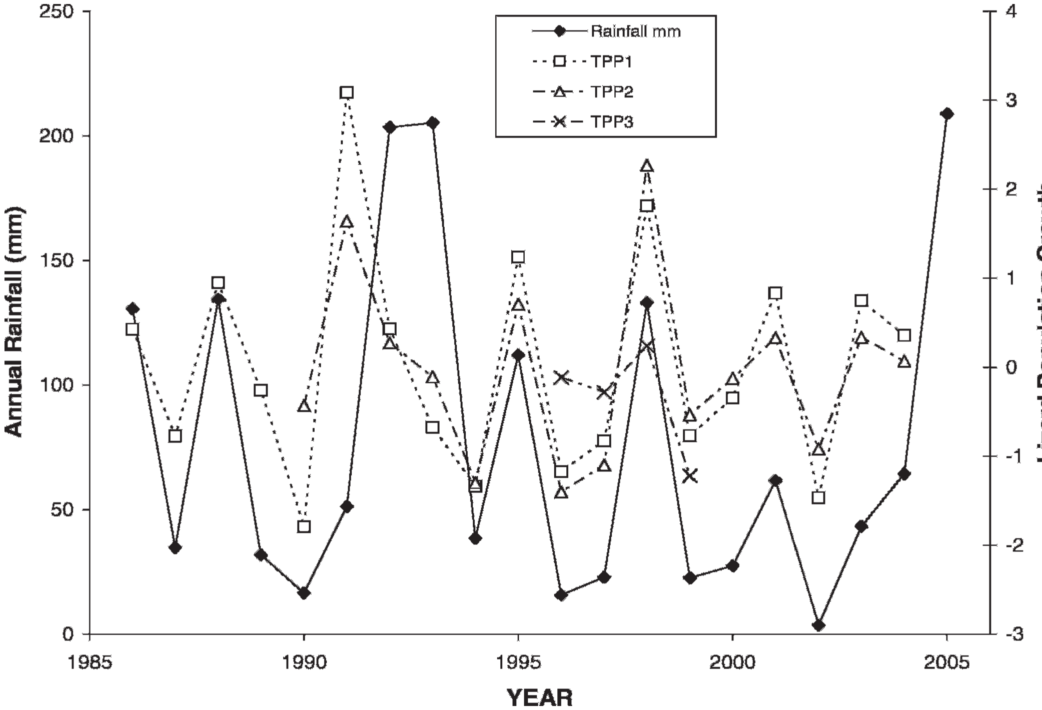

FIG. 1—Time series depicting the relationship between annual rainfall and population growth ($\bar{r}$) for the Coachella Valley fringe-toed lizard (*Uma inornata*) for the July through June rain year at 3 sites in the Thousand Palms Preserve, Riverside County, California.

Survey Protocols—The TPP1 and TPP2 plots are belt transects 1,000 m $\times$ 10 m. The small size of the available habitat at TPP3 did not allow the use of identical survey protocols; here the total habitat area was surveyed using a wandering transect. Area of surveyed habitat was the same on all plots. The number of repeated surveys required per year was determined using a Power Analysis with a standardized effect size of 3.3 and standard deviation of 1.5 (15-year mean, $\alpha = 0.05$, $\beta = 0.80$). Survey data were comprised of counts of *U. inornata* observed within the transects. Transects were surveyed at least 6 times per year in a spring (May–June) census.

In 1990, an autumnal census period (September–October) was added to the TPP1 and TPP2 plots to include young of the year, which emerge between July and September (Mayhew, 1966). TPP1 and TPP2 transects were surveyed an additional 6 times per year in September and October. On the TPP3 plot, a complete census was conducted 8 to 10 times during the same autumnal census period as at the TPP1 and TPP2 sites. Plant density and species richness were measured by counting all perennial plant species on the plots. Rainfall totals for the rain year (July through June) were recorded from a rain gauge on the Thousand Palms Preserve and at the nearby Indio Fire Station.

Data Analyses—The observed mean annual rate of lizard population increase ($\bar{r}$) was calculated using $\bar{r} = \ln(N_{i+1}/N_i)$ where N_i is the mean count of lizards observed during spring surveys in year i.

I analyzed fecal pellets (scat) to determine diet composition at all study locations. Scats were collected monthly (March through June) on and adjacent to the 3 plots from March 1996 through October 2002. This noninvasive method (Pietruszka et al., 1986, and references therein) was used because of the protected status of the lizard and the unknown consequences of repeated captures and disruption on normal lizard activities. Scat from adult *Uma* is distinguishable from scat of sympatric lizard species by shape and size. Any scat of uncertain origin was discarded. Plant content in scat consisted of seeds, leaf fibers, and flower parts. Seed numbers could be identified in the scat, but most plant material could not be quantified with confidence as to the number of leaves or flowers consumed. Therefore, plant frequency was quantified as present or absent in each scat. For statistical analyses, invertebrate frequencies were quantified based on the proportion of the diet of the lizard (not including plants) for taxonomic groups (Formicidae, Coleoptera, Orthoptera, etc.). Diet analyses are confined to those data collected during the spring (March through June) season, the period when the lizards should be preparing for reproduction. Prey proportions were transformed (arcsine transformation yielded the best normal distribution approximation) before inclusion in statistical analyses that required normal data distributions.

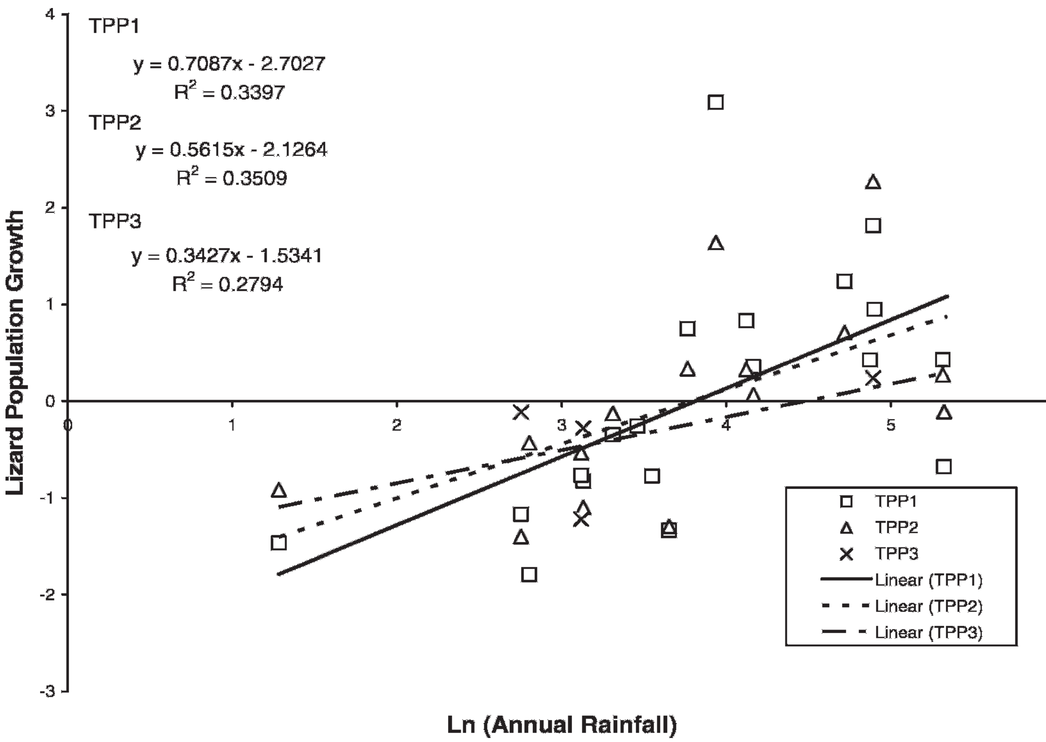

FIG. 2—Relationship of natural log transformed annual rainfall versus population growth ($\bar{r}$) for the Coachella Valley fringe-toed lizard (*Uma inornata*) at sites in the Thousand Palms Preserve, Riverside County, California.

Multivariate models including rainfall and diet variables were limited as to the number of independent variables that could be included due to the number of years when both diet samples and rainfall were recorded. Combining TPP1 and TPP2 yielded an $n = 14$. To create a model that allowed statistical inference, the number of variables needed to be limited so that the variable to observation ratio was $\leq$ 1:7 (Tabachnick and Fidell, 2001); models were, therefore, limited to 2 independent variables. Statistical analyses were performed using Systat 10.0 (SYSTAT, Wilkinson, 1990). A threshold of $\alpha = 0.05$ for statistical significance was used.

RESULTS—With rare exceptions, annual rainfall dynamics coincided with fluctuations in measures of population growth, $\bar{r}$, for each site, (Fig. 1). While the direction of the correlation between $\bar{r}$ and annual rainfall was consistent, the amplitude of $\bar{r}$ with regard to rainfall was less predictable, and so the correlation between these parameters was relatively low, but significant for the 2 sites with the longest data record. For the 3 sites, $R^2 = 0.349$, $P = 0.012$ for TPP1; $R^2 = 0.354$, $P = 0.032$ for TPP2; and $R^2 = 0.279$, $P = 0.471$ for TPP3. When annual rainfall exceeded 40 to 50 mm, there was a shift from a negative to positive $\bar{r}$ at all 4 sites (Fig. 2). Although there are limited data for corroboration, it seems that at annual rainfall amounts >200 mm, there might be a shift back to negative $\bar{r}$.

TPP1 and TPP2 differed from TPP3 in vegetation and food resources available to the lizards. The TPP1 and TPP2 plots were similar, with a sparse, perennial shrub density of 134 plants/ha and 70 plants/ha, respectively. Just 3 shrub species were present on these plots; creosote bush comprised 13% and 63%, and saltbush constituted 87% and 37%, respectively, of perennial shrubs at the 2 sites. The juxtaposition of plot TPP3 with a natural palm oasis and upwelling groundwater along the San Andreas earthquake fault resulted in a much more mesic environment, with a perennial shrub density of 331 plants/ha. Five shrub species comprised the perennial vegetation community, with creosote bush at 2%, saltbush at 73%, arrowweed at 17%, alkali goldenbush (*Isocoma acradenia*) at 5%, and honey mesquite at 3% of the total composition.

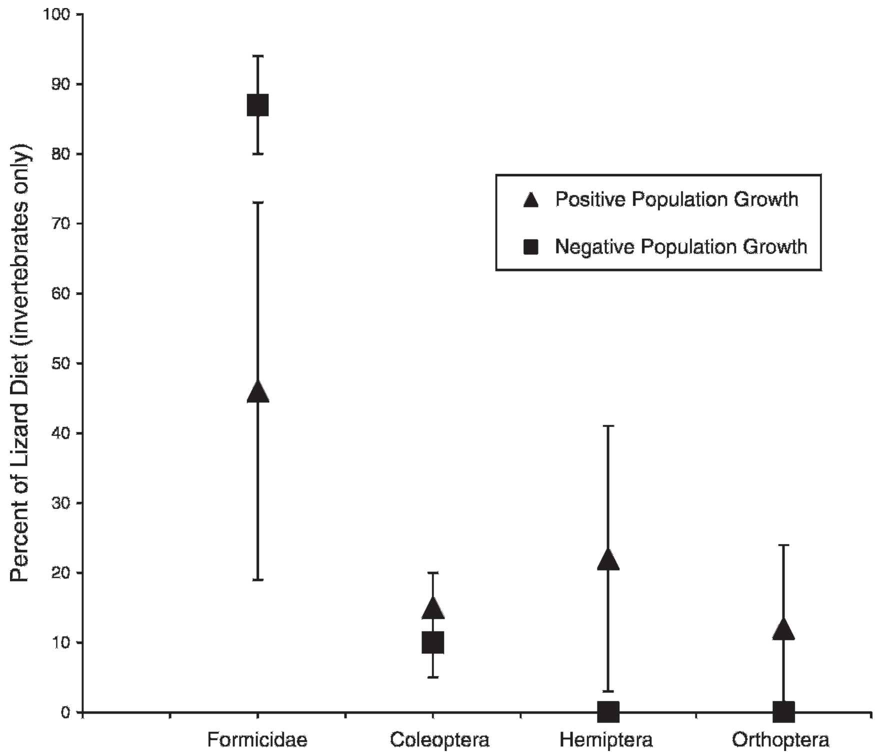

FIG. 3—The proportion of 4 diet categories at the combined TPP1 and TPP2 sites in the Thousand Palms Preserve, Riverside County, California, showing the difference in fringe-toed lizard diets between years with positive and negative population growth ($\bar{r}$) for the Coachella Valley fringe-toed lizard (*Uma inornata*).

At all TPP plots, long-lived annuals or biennials, such as bugseed (*Dicoria canescens*) and coldenia (*Tiquilia plicata*), were present only in the wettest years.

A total of 701 *U. inornata* scats were collected at the TPP1 and TPP2 plots over a 7-year span (scats contained 7,758 arthropod prey items); 374 scats were collected on the TPP3 plot over 5 years (scats contained 2,676 arthropod prey items). Frequencies of plants, ants, and other invertebrates consumed varied between years of positive and negative population growth (Fig. 3). Population growth ($\bar{r}$) was positive for only 2 of the 7 years that I collected diet data.

Diet shifts between positive and negative $\bar{r}$ years were seen on the TPP1 and TPP2 plots. The proportion of lizard scats with plants and with harvester ants (*Pogonomyrmex*) differed ($U_{0.05\ (1)\ 2,\ 5} = 10$, $P < 0.05$), with more plants and fewer ants ingested during years of positive $\bar{r}$ than years of negative $\bar{r}$. No statistically significant differences in the proportion of plant to invertebrate prey were detected on the TPP3 site. However, data collection on TPP3 was curtailed 2 years earlier than expected because this population became extirpated. Pairwise Pearson's correlation values for 4 diet variables, rainfall, and population growth at the TPP1 and TPP2 plots are shown in Table 1.

Due to overall similarity between patterns of response to rainfall and diet variables, TPP1 and TPP2 data were combined to create a multivariate model to explain the variance in population growth at these sites. Annual rainfall and the proportion of harvester ants in the lizard diets were the variables that had the most consistent (between plot) and strongest correlation with the lizard population growth (Table 1). The resultant multivariate, linear regression model yielded an $R^2 = 0.956$, $P < 0.0001$. The availability of phytophagous arthropods, such as species of Hemiptera and Othroptera, were not measured, but were likely correlated with percent annual plant cover, which in turn was highly correlated to annual rainfall ($R^2 = 0.999$, $P = 0.007$). These insects were important food items

TABLE 1—Pearson's correlation coefficients relating Coachella Valley fringe-toed lizard (*Uma inornata*) population growth ($\bar{r}$) to diet variables and precipitation at 3 sites in the Thousand Palms Preserve, Riverside County, California.

Variables	TPP1	TPP2	TPP3
Annual rainfall	0.933	0.806	0.529
Ants	−0.742	−0.848	−0.723
Beetles	−0.057	−0.025	0.412
Invertebrates (minus ants)	0.624	0.806	0.686
Plants	0.516	0.310	−0.217

for fringe-toed lizards during wet years and when the lizard population growth was positive (Fig. 3). However, the abundance of harvester ants was measured and was not correlated with rainfall ($R^2 = 0.022$, $P = 0.728$). Additionally, the proportion of the diet of the lizards consisting of harvester ants revealed only a weak negative correlation with increasing rainfall ($R^2 = 0.244$, $P = 0.073$). The lack of a strong correlation between ant abundance and rainfall indicated these 2 variables are independent. When lizard population growth was regressed against rainfall and the proportion of ants in their diet as univariate models, the correlation coefficients were much weaker ($R^2 = 0.346$, 0.697, respectively) than was the multivariate model.

DISCUSSION—The relationship between annual rainfall and population growth for Coachella Valley fringe-toed lizards is consistent with that for other desert lizard species (Mayhew, 1965; Pianka, 1970; Ballinger, 1977; Whitford and Creusere, 1977; Seely and Louw, 1980; Dunham, 1981; Abts, 1987; Robinson, 1990; Brown and Ernest, 2002; Castañeda-Gaytán et al., 2003). Even small fluctuations in annual rainfall corresponded to parallel demographic changes for fringe-toed lizards. Although statistically significant positive linear correlations between rainfall and population growth were measured, this relationship might not extend to high rainfall years. At the highest rainfall levels recorded, the population growth of the lizards declined. While a fit with a linear model was statistically significant, the relationship between rainfall and the population growth of the lizards might not be truly linear; rather there might be a rainfall threshold at about 40 to 50 mm, above which sufficient resources are present to enable positive population growth.

During dry years, harvester ants dominated the diets of the lizards, and the lizards often appeared extremely thin. I examined differences in the diets of the lizards with respect to their population growth. If rainfall patterns produced enhanced resource abundance and availability, the result should be reflected in the diets of the lizards. For the 2 sites with the sparsest perennial vegetation, diet differences between years of high positive and negative population growth were significant. Combining precipitation and the proportion of ants in the diets of the lizards into a multivariate model explained over 95% of the variance in population growth over a 7-year period. During years of higher rainfall, the lizards ate relatively more annual plants and larger, phytophagous invertebrates, primarily species of Hemiptera and Orthoptera. Reproduction during these years increased. At a finer scale, (Durtsche, 1992) described a similar shift in foraging strategies by female *U. inornata* during the breeding period in spring. Such a foraging strategy would increase fat deposition rates and increase the reproductive success of the lizards (Robinson, 1990). The increased abundance of annual plants and arthropods in wetter years provides lizards with a greater array of food choices. Previous studies analyzing fringe-toed lizard diets have suggested that the lizard diets reflect available resources (Durtsche, 1992, 1995; Gadsden and Palacios-Orona, 1997).

The shift to negative population growth when annual rainfall exceeded 200 mm seems inconsistent with the hypothesis that higher rainfall leads to increased annual plants, increased arthropods, and then increased lizard reproduction. Several hypotheses could explain this response to high precipitation levels. Andrews and Wright (1994) determined experimentally that an extended period of above average rainfall resulted in a population decline due to reduced egg viability in a tropical lizard. Extremely moist conditions in the egg chamber can cause increased infections by fungi and microorganisms (Tracy, 1980) or reduced gas exchange (Packard and Packard, 1984). Additionally, the assumption that the relationship between rainfall and food resource abundance is linear at the higher rainfall levels might not be correct. High rainfall (approximately 210 mm) in 2005 did not result in increased abundance in harvester ants or beetles on the sand dune habitat (Barrows, unpubl. data).

Coachella Valley fringe-toed lizards were observed exhibiting negative population growth 10 out of the 20 years of my study. The population dynamics described here are consistent with a non-equilibrium paradigm (Picket et al., 1992), where population levels reflect stochastic changes in resource availability. Given that drought is common in arid environments, it is not unusual for this species to endure consecutive years of population declines. During extended droughts, mean population counts often approached zero, yet the populations quickly rebounded during periods of near average rainfall. From the standpoint of developing a meaningful monitoring program, counts approaching zero, or consecutive years of negative population growth are, thus, not reliable thresholds for when remedial management actions are warranted to maintain the continued viability of this population. Monitoring-based management decisions need to use criteria that are more heuristic.

Maintaining viable populations of endangered species in highly variable environments presents a unique challenge. Such populations can be stressed by fragmentation (Saunders et al., 1991; Martin and McComb, 2003; Chen et al., 2006), compromised processes maintaining suitable habitat (Barrows, 1996), invasions of exotic species (Atkinson, 1989), and changes in predator population composition and density (Crooks and Soule, 1999), among other factors. Addressing these stressors or their effects through remedial management might be critical to the continued existence of endangered species. Thus, identifying when the stressors are negatively impacting the populations should become a focus of monitoring activities. Separating natural population dynamics from anthropogenic stressor effects can be difficult without a conceptual and quantitative framework from which to evaluate population changes. Departures from the rainfall-diet-population growth model might provide the signal needed for management actions. The influence of potential population stressors, such as population isolation or the invasion of exotic vegetation, could be interpreted as to the magnitude of departure from the regression model. Without this conceptual context, with empirical support, managers charged with insuring that lizard populations persist would have difficulty discerning when management actions are warranted. Developing models to explain natural population variance so that departures from those models can be identified should be a critical conservation goal for any species at risk of extinction.

The extinction of the fringe-toed lizard population on TPP3 during the course of this study provides an example of how this dynamic model based approach could be employed. By tracking both the lizard population growth and diet along with habitat conditions, causal factors, such as demographic bottlenecks, exotic weed infestations, predation, and habitat degradation, could be evaluated. This site consisted on a single dune roughly 1 ha in size, separated by other *Uma* populations and other suitable habitat by at least 6 km. As the leading edge of this active dune moved into a natural palm oasis, predatory birds, such as American kestrels, *Falco sparverius*, and loggerhead shrikes, *Lanius ludovicianus*, sitting in the palm trees easily preyed upon any lizard that ventured on to the avalanche face of the dune. A dune avalanche face with its loosely compacted sands is a preferred habitat for Coachella Valley fringe-toed lizards (Barrows, 1997) and was regularly visited by all members of this small population; within one year, the population was extinct. As long as the dune avalanche face is adjacent to the palm trees, this site will remain unsuitable for occupancy by the lizards. A dynamic model based approach to monitoring, coupled with evaluations of potential threats provided an unambiguous cause and effect explanation for the decline of this lizard population. It then becomes a management question as to whether it is possible and appropriate to change that trajectory. In this situation, the dune provided $<<1\%$ of the remaining habitat for the fringe-toed lizards, and the palm oasis and native predatory birds were deemed valuable components of the overall landscape; no management action was taken.

In a related example elsewhere on the Thousand Palms Preserve, the same 2 avian predators were implicated in a decline of flat-tailed horned lizards, *Phrynosoma mcallii*, (Barrows et al., 2006). A population model was used to demonstrate that the predators were responsible for a decline of the horned lizards that was in excess of an otherwise modeled/predicted population decline. Here the avian predator population and impacts were enhanced by power-line perches and nesting sites in exotic vegetation growing in surrounding suburban neighborhoods and golf courses. Management options included removing the power lines and trimming exotic vegetation to remove potential nest sites.

The Thousand Palms Preserve, where my research was focused, is a remnant of a once extensive sand dune ecosystem (Barrows, 1996). The fragmented nature of the remaining protected habitat begs questions as to the long-term viability of these populations. Chen et al. (2006) modeled the long-term viability of *U. inornata* on the same plots I have described in this analysis. They determined that on isolated habitats <100 to 200 ha in size, long-term viability of this species was doubtful. Certainly, the extinction of the TPP3 population is consistent with that prediction. The TPP1 and TPP2 plots occurred on sand dunes that were each less than 60 ha, but occurred in a mosaic of sand dunes that totaled about 250 ha. These dunes were imbedded in a matrix of interdune, sand hummock habitat where fringe-toed lizards also occurred, albeit in low densities. The lizards could easily travel between the higher quality sand dune habitats. The total occupied habitat was closer to 750 ha, and so the prospects for long-term persistence for the TPP1 and TPP2 plots might be more secure than a focus on only the individual habitat patches where the plots were located would indicate. Nevertheless, ongoing monitoring of these sites, using the dynamic context I have provided here, will provide early detection and, thus, an opportunity for remedial response if habitat fragmentation becomes a population stressor here.

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