A Historical Resurvey of Flatland Lizards in the Mojave Desert

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Abstract

Historical resurveys are uniquely valuable for the information that they provide regarding population responses to environmental changes. As anthropogenic impacts on the environment proceed, such efforts are becoming increasingly important for developing a historical baseline and for understanding how contemporary populations respond. We undertook a >50-year historical resurvey of the Mojave Desert flatland lizard community by pairing data from the 1960s and today, which provided a repeatable benchmark for future monitoring. We found few changes in distribution, with at least 9 of 11 species continuing to occur where they were previously detected. However, we found marked declines in abundance for the widespread and highly detectable Side-blotched Lizard (*Uta stansburiana*), one of three species where data were sufficient to robustly estimate abundance. Both our work and other recent works highlight the difficulty of estimating abundance for wild lizard populations and, should we wish to understand declines before they turn into extirpations, call for the continued development of methods for efficient and robust tracking of desert reptile populations.

Historical surveys provide a rare snapshot from which to follow change in communities over time, often in ways that past researchers could never have anticipated. Here we add another case study for documenting community change: Eric Pianka's surveys of flatland lizard communities in North American deserts. Pianka's 1965 dissertation was an early exploration of drivers of community structure across a latitudinal gradient and helped solidify lizards as fruitful study systems for ecological and evolutionary questions (Pianka, 1965). Here, we focus on how those populations in the Mojave Desert have fared over time.

The Mojave Desert has changed considerably since the 1960s. There have been dramatic and ongoing increases in development from renewable energy installations, roads, growing human populations, spread of introduced species, and a rapidly changing climate (Berry et al., 2006; Carter et al., 2020; Mirzabaev et al., 2022; S. S. Parker et al., 2018; Randall et al., 2010; Smith et al., 2023). The handful of resurveys available show that animal communities are being affected by human impacts. In contemporary protected areas, mammal communities have been relatively stable from the mid 20th century compared to today, while birds have declined dramatically in distribution and local richness (Iknayan & Beissinger, 2018; Riddell et al., 2021). For reptiles, recent resurveys of lizards in Joshua Tree National Park, when compared to the 1950s–1970s, showed evidence for elevational shifts in some taxa that were consistent with climate change (Barrows et al., 2016, 2020). Warming and increased aridity can negatively affect desert lizards directly based on their physiological tolerances and life histories, and indirectly through impacts on vegetation, prey, and wildfire risk. Wildfire regimes are also impacted by introduced grasses (Brooks, 1999), the spread of which affect lizard habitat. Development poses risks to lizards through multiple mechanisms such as habitat loss, habitat fragmentation, spread of introduced species, subsidizing of predators, and vehicle mortality due to roads and off-highway vehicles (Boarman, 2003; J. E. Lovich & Ennen, 2011; Luckenbach & Bury, 1983; Ouren et al., 2007; Pavlik, 2008; Walker & Landau, 2018). Recent and planned renewable energy development is of particular concern for lizards and has already led to the downgrading of overall habitat quality in the Western Mojave and Ivanpah Valley (S. S. Parker et al., 2018). Considering the threats imposed by humans, Pianka's historical data provide an opportunity to ask whether distribution and abundance of Mojave Desert lizards has changed over time.

Resurveying Pianka's sites is challenging because desert reptiles are notoriously difficult to monitor. They are small, often camouflaged, readily flee, or alternatively cryptically freeze, and their surface activity is limited by abiotic conditions. In addition, methods for estimating abundance have changed over time. Pianka (2017) acknowledged that the methods he initially used as a graduate student were not ideal and used more standardized approaches in his later desert lizard research. Despite limitations on censusing desert reptiles, data on lizard abundance, whether historical or contemporary, are uncommon but critical for detecting population declines. We have not exactly duplicated Pianka's methods, but instead used complementary and modern approaches. Our goals were to document changes that have occurred and to provide a repeatable benchmark for future monitoring.

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Materials and Methods

We resurveyed the 5 Mojave Desert sites sampled by Pianka in 1963 and 1964 for 11 focal flatland desert lizard species (Tables 1, S2). The localities with his original codes in parentheses are Grapevine Canyon (V), Pahrump (P), and Searchlight (S) in Nevada, and Mojave (M) and Twentynine Palms (T) in California (Fig. 1). We also surveyed three new sites in California, two in the Kingston Mountains, and one at Pisgah Crater (Fig. 1, Table S2). Pianka provided coordinates for each site, and plots ranged in area from 15.5–51.8 km^2 (Pianka, 1965, Table 3). Pianka searched for lizards for days within each site, often with repeated visits over the activity period, and his index of lizard abundance was the number of lizards seen per distance covered as recorded by a pedometer. A key limitation of Pianka's approach was that it did not account for detection probability, and therefore can only provide a measure of relative, and not absolute, abundance (Mazerolle et al., 2007; Pollock et al., 2002). The methodology of abundance estimation has developed extensively since Pianka's surveys (Buckland et al., 2000). We conducted visual encounter distance line transect surveys, which formally account for detection probability and can provide robust abundance estimates if assumptions (e.g., 100% detection of animals on the transect line, lack of movement prior to detection, distances are measured accurately, independent sightings of individuals) are met and sample sizes are adequate (~60–80 detections) (Buckland et al., 2001; Burnham & Anderson, 1976; Elphick, 2008). In addition to providing measures of absolute abundance, distance methods for sampling reptiles provide standardization of effort and location, particularly for long-term studies (R. E. Lovich et al., 2012), and are therefore more repeatable than the approach used by Pianka.

We conducted our surveys in late May and early June, with 90% of surveys occurring between 0700 and 1100 hours. Each site was visited a maximum of once per year, with all transects sampled over 1–3 consecutive days. We surveyed Grapevine in 2017 and 2022, Pisgah Crater in 2016, and all other sites in every year (2015, 2016, 2017, and 2022). We used a similar visual encounter transect design as has been used by other desert lizard researchers (Barrows et al., 2016; Furnas et al., 2019; Heaton et al., 2006). On each survey, the same 4 observers lined up 25 m apart and walked parallel transects following the same compass bearing for 500 m. Each survey covered 2 km total (4 observers × 500 m), and we conducted 3–6 surveys within each site during every year visited (6–12 km per site per year, 214 km total; Tables S1, S2). For every lizard seen, observers recorded the species identity and the perpendicular distance between the lizard and the transect. Distances for spacing observers and for the transect length were measured by GPS. In the rare occurrence that a lizard ran from one observer's transect to another, the movement was communicated to prevent double counting of individuals. In addition to distance surveys, we also searched each plot extensively on all visits to document occurrence and to collect tissue and voucher specimens. To compare species distribution over time, we included all species documented within each site during surveys and collections across all years visited.

We estimated density using distance models for the three species with an adequate number of detections to fit models: Western Whiptail Lizards (*Aspidoscelis tigris;* hereafter Whiptails), Side-blotched Lizards (*Uta stansburiana*), and Zebra-tailed Lizards (*Callisaurus draconoides*). We fit distance models separately for each species following the methods of Royle et al. (Royle et al., 2004) using the package *unmarked* (Fiske & Chandler, 2011) in R Version 4.1.2 (R Core Team, 2021). We used AIC to choose the best detection function for each species. Models included year (2015–2017, 2022) and site (all five historical sites plus three additional contemporary sites) as abundance covariates, and observer as a detection covariate.

To test whether abundance has changed over time, we compared density estimates from distance models with densities reported by Pianka (1965) for Whiptails and Side-blotched Lizards (other lizards did not have historical abundance data). Pianka provided density estimates for both species at Grapevine, Mojave, Searchlight, and Twentynine Palms, but only for Whiptails from Pahrump. We used the average for each year to represent past density because it was provided for both Whiptails (Pianka, 1965, Fig. 11, annotated points) and Side-blotched Lizards (Pianka, 1965, Table 18), and because seasonal means were similar to May–June values, which is when contemporary data collection occurred. To compare abundance over time, we used mixed models fit in the package *lme4* (Bates et al., 2015) and conducted hypothesis tests using the package *lmerTest* (Kuznetsova et al., 2017) in R Version 4.1.2 (R Core Team, 2021). We fit separate models for each species with time period (past vs. current), site, and their interaction as fixed predictors, and year as a random effect. For each species, our statistical models tested whether there is a difference in abundance when comparing past vs. current time periods, whether there is a difference in abundance across sites, and whether the degree of change between past and current abundance varies across sites (i.e., are there declines at some sites but not others?). Year is included as a random effect to account for similarities among sites sampled in the same year, given that climate varied between years (Fig. 1) and year effects on lizard abundance in arid environments can be large. Sampling year cannot be included as a fixed effect because it is nested within time period.

To document observed climate change over time, we downloaded annual precipitation and mean annual temperature data from PRISM (https://prism.oregonstate.edu, accessed May 2023) for the years with lizard abundance data (past: 1963, 1964; present: 2015, 2016, 2017, 2022). To visualize changes over time across the entire Mojave Desert, we calculated the average for each cell across years within each time period, then calculated the difference as (present − past). Positive values in the difference between present and past mean annual precipitation indicated that it is currently wetter than it was in the past, whereas negative values indicated that it is currently drier. For mean annual temperature, positive values between present and past means indicated that it is currently warmer than it was in the past, whereas negative values indicated that it is currently cooler. At the site level, we visualized annual variation as well as averages within time periods. We calculated averages first at

TABLE 1. Species richness and composition.

	Grapevine	Mojave	Pahrump	Searchlight	Twentynine Palms	Kingston West	Kingston East	Pisgah Crater
Western Whiptail Lizard *Aspidoscelis tigris*	1,1	1,1	1,1	1,1	1,1	NA,1	NA,1	NA,1
Side-blotched Lizard *Uta stansburiana*	1,1	1,1	1,1	1,1	1,1	NA,1	NA,1	NA,1
Long-nosed Leopard Lizard *Gambelia wislizenii*	1,1	1,1	1,1	1,1	1,1	NA,1	NA,1	NA,0
Desert Horned Lizard *Phrynosoma platyrhinos*	1,1	1,1	1,1	1,1	1,1	NA,1	NA,1	NA,1
Zebra-tailed Lizard *Callisaurus draconoides*	1,1	1,1	1,1	1,1	1,1	NA,1	NA,1	NA,1
Western Banded Gecko *Coleonyx variegatus*	1,0	1,1	1,1	1,1	1,1	NA,0	NA,0	NA,0
Desert Iguana *Dipsosaurus dorsalis*	0,0	0,0	1,1	0,0*	1,1	NA,1	NA,0	NA,1
Desert Spiny Lizard *Sceloporus magister*	0,0	1,1	0,0	0,0	0,0	NA,1	NA,1	NA,0
Long-tailed Brush Lizard *Urosaurus graciosus*	0,0	0,0	0,0	0,0*	1,1	NA,0	NA,0	NA,1
Mojave Fringe-toed Lizard *Uma scoparia*	0,0	0,0	0,0	0,0	1,0	NA,0	NA,0	NA,0
Desert Night Lizard *Xantusia vigilis*	0,0	1,1	0,0	0,0	0,0	NA,1	NA,1	NA,0
Total richness								
1963–1964	6	8	7	6	9	NA	NA	NA
2015–2022	5	8	7	6	8	8	7	7

1,1 = species present both time periods; 0,0 = species absent both time periods; 1,0 = species present in the 1960s and absent in the current time period; NA,1 = species present in current time period and sites not sampled in the 1960s; NA,0 = species absent in current time period and sites not sampled in the 1960s. * Indicates species documented near plot boundary.

RESULTS

We found that most species (9 of 11) still occur where Pianka documented them (Table 1). The exceptions were Mojave Fringe-toed Lizards (*Uma scoparia*) and Western Banded Geckos (*Coleonyx variegatus*), which we did not detect at Twentynine Palms and Grapevine, respectively (Table 1). As a result, these two sites showed a reduction in richness of one species, while the other three sites were unchanged (Table 1). We documented two focal species near the Searchlight plot that were not recorded by Pianka: Desert Iguanas (*Dipsosaurus dorsalis*; 0.6 km away) and Long-tailed Brush Lizards (*Urosaurus graciosus*; 1.3 km away). Vouchers were deposited at the Natural History Museum of Los Angeles County (Desert Iguanas: LACM 189061; Long-tailed Brush Lizards: LACM 187011–187014, 188126–188128, 189057–189060).

We observed a total of 800 individual lizards on distance surveys at the 8 sites (5 historical sites plus 3 additional sites; Table S3). The most frequently detected species were Side-blotched Lizards (322), Whiptails (296), and Zebra-tailed Lizards (140). Four species were rarely seen on distance surveys: Long-nosed Leopard Lizards (*Gambelia wislizenii,* 10), Desert Iguanas (*Dipsosaurus dorsalis*, 4), Desert Spiny Lizards (*Sceloporus magister,* 6), and Desert Horned

Lizards (*Phrynosoma platyrhinos,* 1). The following focal species were not detected on distance surveys: Desert Night Lizards (*Xantusia vigilis*), Western Banded Geckos, Mojave Fringe-toed Lizards, and Long-tailed Brush Lizards. We saw two species on surveys at Pahrump that were not focal species: Great Basin Collared Lizards (*Crotaphytus bicinctores*, 7) and Chuckwallas (*Sauromalus ater*, 4). In 10 cases we were unable to identify the lizard to species (~1% of observations).

Side-blotched Lizards were less abundant compared to the 1960s (time period: $F_{1,12}$ = 10.5, P < 0.01; Figs. 2A, 2C), and this pattern was driven by extreme rarity at Mojave, Searchlight, and Twentynine Palms (time period*site interaction: $F_{3,12}$ = 12.9, P < 0.001; Figs. 2A, 2C). Side-blotched Lizards were only seen in one of the 4 years at each of these sites (observed in 2022 at Mojave and Twentynine Palms and 2017 at Searchlight). Sites did not differ overall in Side-blotched Lizard density (site: $F_{3,12}$ = 2.4, P = 0.12; Figs. 2A, 2C) and the random effect for year did not explain any additional variation in density beyond what was accounted for by time period. By contrast, Side-blotched Lizards achieved high contemporary densities at the other historical site, Pahrump, as well as in the Kingston Mountains—up to more than eight times higher than reported by Pianka for Mojave Desert sites in the 1960s (Figs. 2, 3).

Whiptail densities were similar between past and current data (time period: $F_{1,4.6}$ = 1.5, P = 0.28; Figs. 2B, 2D). There were large differences in Whiptail abundance across sites,
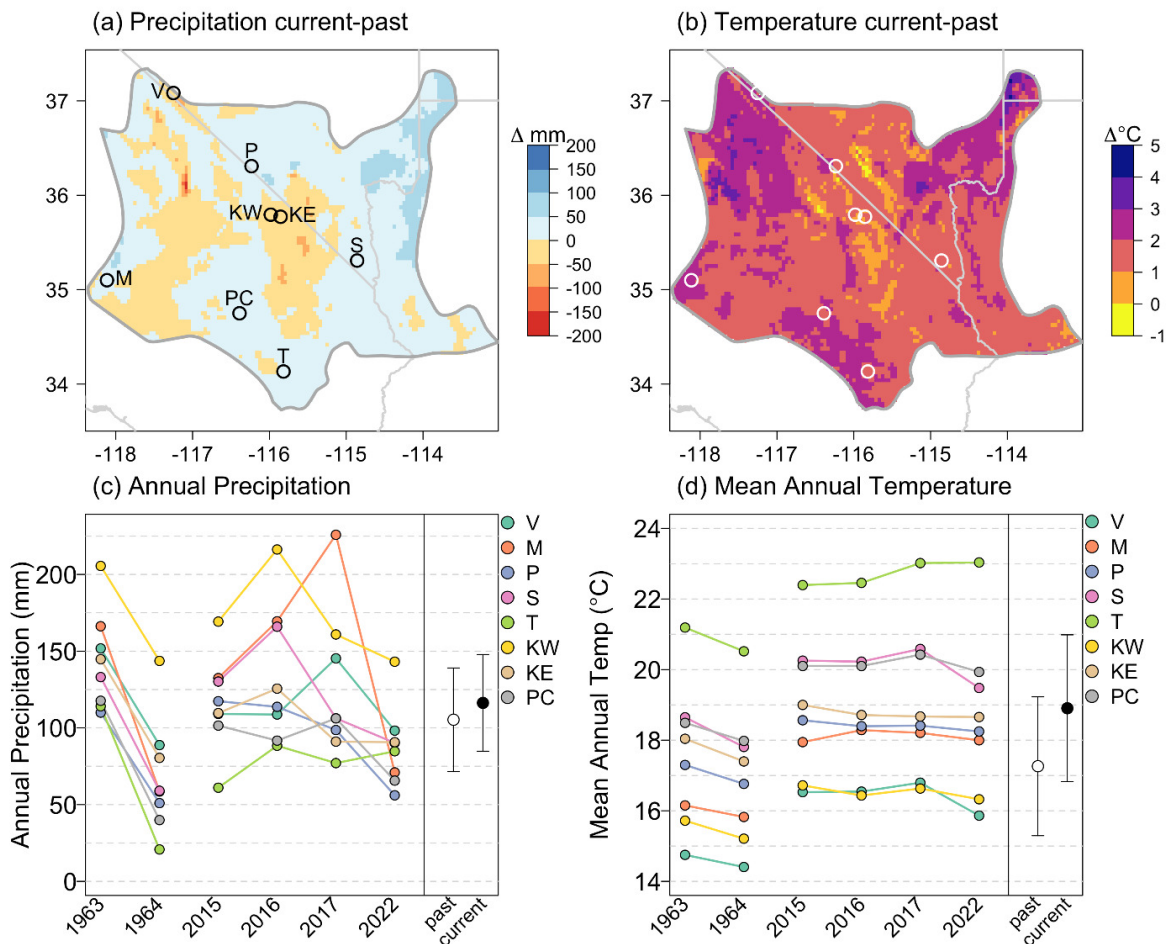
FIGURE 1. Observed climate changes in the Mojave Desert.

Top panels (A–B) show differences in (A) Annual Precipitation and (B) Mean Annual Temperature between mean current conditions (2015–2017, 2022) and mean 1960s conditions (i.e., "past", 1963–1964). Positive values indicate increases over time (i.e., wetter or hotter); negative values indicate decreases over time (i.e., drier or cooler). Circles are study sites; clockwise from northernmost site and labeled in (A): Grapevine (V), Pahrump (P), Kingston West (KW), Kingston East (KE), Searchlight (S), Twentynine Palms (T), Pisgah Crater (PC), Mojave (M). Axes are latitude and longitude, and thin borders are state boundaries. Bottom panels (C–D) show annual values from the 1960s and current time periods in color for each site, with the mean ± SD in black and white. Means were calculated by averaging across years within sites for the 1960s and current time periods, then averaging across sites within time periods.

with Searchlight and Mojave having the highest densities (site: $F_{4,11.5}$ = 20.0, P < 0.001) and this was true across time periods (i.e., the effect of site did not vary over time: time period*site interaction: $F_{4,11.5}$ = 1.4, P = 0.29; Figs. 2B, 2D). In addition to strong site differences, there were also year effects driven by very high densities in 2017 and very low densities in 2022 (Fig. 3B).

Side-blotched Lizard detections were best fit with an exponential function, while detections for other species were best fit with a hazard function (Fig. S1). Detection varied slightly among observers for Side-blotched Lizards, but not for Whiptails or Zebra-tailed Lizards (ΔAIC model with vs. without detection varying by observer: Side-blotched Lizards 68, Whiptails 0.34, Zebra-tailed Lizards 2.7; Fig. S1). The effective half-strip width averaged among the four observers for each species was: Side-blotched Lizards 2.5 ± 1.0 m, Whiptails 2.8 ± 0.3 m, Zebra-tailed Lizards 4.1 ± 0.5 m (mean ± SD, Fig. S1). Thus, the total transect width within which we effectively surveyed lizards ranged on average from 5–8.2 m, which is similar to the 6.1–7.6 m reported by Pianka (Pianka, 1965, p. 43).

Annual precipitation in the Mojave Desert during years with lizard abundance data has shown both increases and decreases over time, with most sites experiencing changes of ± 50 mm (Figs. 1A, 1C). By contrast, there has been a clear overall warming trend in the Mojave Desert during the study period, with the average increase being 1.8 °C warmer (Figs. 1B, 1D). At our specific study sites, the range of variation among sites was similar over time, and all sites were warmer now than in the 1960s (Fig. 1D). The largest increases (1.9–2.1 °C) were seen at Grapevine, Twentynine Palms, Pisgah Crater, Searchlight, and Mojave, whereas other sites experienced average warming of 1.0–1.4 °C (Fig. 1D).

DISCUSSION

Most species still occur everywhere that Pianka observed them, and for the two that we did not detect, we are only confident in the loss of Mojave Fringe-toed Lizards at Twentynine Palms. Our conclusion that Mojave Fringe-toed Lizards are now extinct at Twentynine Palms is likely valid because other extirpations of Mojave Fringe-toed Lizards
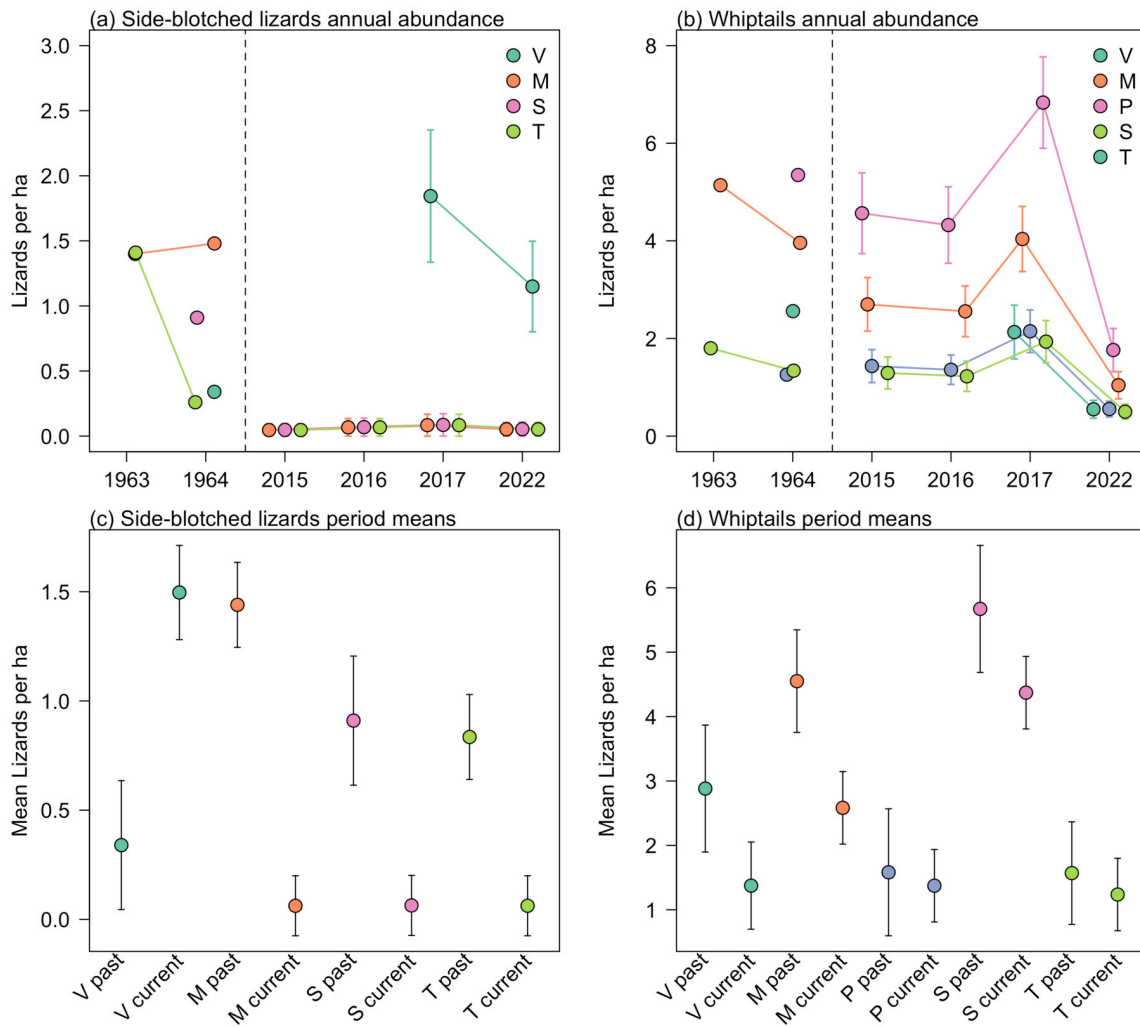
FIGURE 2. Side-blotched Lizard (*Uta stansburiana;* A, C) and Whiptail (*Aspidoscelis tigris*; B, D) abundance over time.

Panels A and B: 1963–1964 data are replotted from Figure 11 and Table 18 in Pianka (1965), and 2015–2022 data are from distance model estimates (± SE). Panels C and D: Model-estimated mean values (± SE) during 1960s (i.e., "past", 1963–1964) and current (2015–2022) time periods. Colors and letter codes are sites: V = Grapevine, M = Mojave, P = Pahrump, S = Searchlight, T = Twentynine Palms. Note that the y-axis scale varies across panels. Past data were unavailable for Side-blotched Lizards at the Pahrump site.
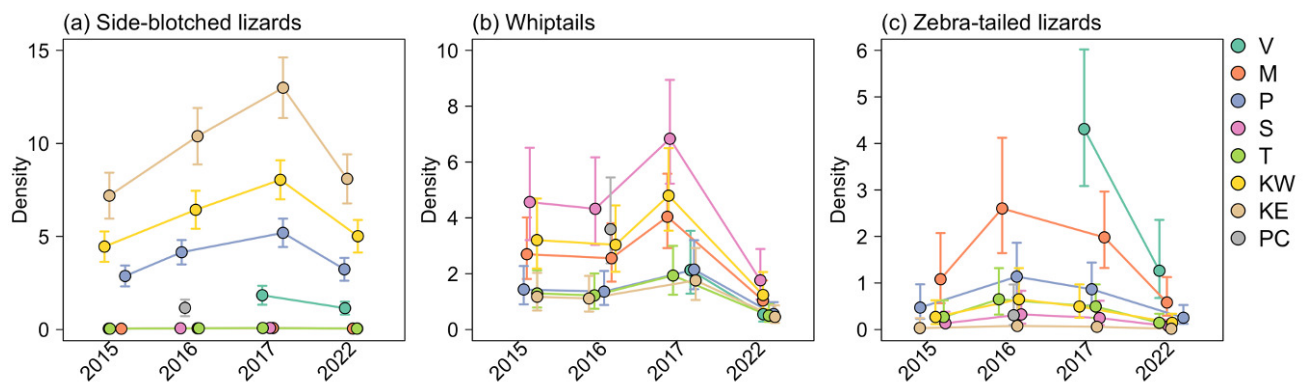

FIGURE 3. Density estimates over time for current sampling from distance models for all study sites.

Units for density on the y-axis are lizards per hectare, and error bars are SE. Note that the y-axis scale varies across panels. Colors and letter codes are sites: V = Grapevine, M = Mojave, P = Pahrump, S = Searchlight, T = Twentynine Palms, KE = Kingston East, KW = Kingston West, PC = Pisgah Crater.

have been suspected (Cablk & Heaton, 2002; Murphy et al., 2006), the species is known to be at risk (Thomson et al., 2016; USFWS, 2011), and the contemporary habitat quality is poor. Fringe-toed Lizards are habitat specialists that

often require loose, wind-blown sand, but we observed extensive hard packed sand throughout the site (Fig. S2). We also observed off-highway vehicle tracks within the site, a known threat to this species through multiple mechanisms (Thomson et al., 2016; Fig. S2). Corroborating our results, prior work (Cablk & Heaton, 2002) noted several cases in the same region where resurveys did not find this species, despite occurrences just a decade or two prior to surveying. However, Cablk and Heaton also observed more Mojave Fringe-toed Lizards in fall compared to summer. Revisiting in the fall would help confirm the absence of Mojave Fringe-toed Lizards at Twentynine Palms. We are less confident in the extirpation of Western Banded Geckos from Grapevine because we only visited the site during two of the years, and we did find them at our campsite ~12.5 km away. In addition, Grapevine is at the highest elevation of Pianka's Mojave sites (1,372 m), and we visited in late May. Additional visits, and visits later in the year when it is warmer at night, would be needed to better establish whether Western Banded Geckos persist at this site.

In addition to our observed potential extirpations, we also documented a potential for increase in richness at the Searchlight, Nevada site. We observed two species that had not previously been documented by Pianka (Desert Iguanas and Long-tailed Brush Lizards) along the road into the study site, leading us to hypothesize that development may be facilitating dispersal. Key developments in this region were the founding of CalNevAri, Nevada (early 1960s, 1 km away), and a now defunct long-range navigation transmitter station (1970s, 4 km away). Desert road edges harvest water, supplementing growth of large creosote bushes (*Larrea tridentata*; Johnson et al., 1975; Lightfoot & Whitford, 1991), which both lizard species use. We also observed Long-tailed Brush Lizards using man-made fence line habitats along the road. Further studies should investigate the role of roads and other human-created habitat corridors in facilitating distributional shifts by desert lizard populations.

We found an overall decline in Side-blotched Lizard abundance compared to estimates made in the 1960s, and this corroborates an observation by Pianka in one of his last papers: "I have returned to Mojave and Twentynine Palms in California … to find nothing at study sites that were once teeming with lizards" (Pianka, 2017). In three out of four years, we saw no Side-blotched Lizards during surveys or collections at Mojave, Twentynine Palms, or Searchlight. We do not think that the apparent decline in abundance of Side-blotched Lizards reflects a failure of survey methods because we observed high densities of Side-blotched Lizards at Pahrump and in the Kingston Mountains using the same methods, and this species is one of the most common and easy to find lizards in this community. The three sites with current low abundance for Side-blotched Lizards appeared to be the most developed compared to our other study sites in terms of roads, wind farms, nearby human habitation, military installations, off-highway vehicle use, and invasive grass cover (Figs. S2–S4). Our observations are largely consistent with recent ecoregional assessments of conservation value showing the most degraded habitat in the western and southern Mojave Desert (S. S. Parker et al., 2018; Randall et al., 2010).

Not all species respond similarly to environmental changes, and other taxa for which we have density estimates achieved high abundances at some of the sites where Side-blotched Lizards are currently rare. Side-blotched Lizards were rare at Mojave and Searchlight, but Zebra-tailed Lizards reached some of their highest densities at Mojave, and Whiptails were at highest abundance at Searchlight. Clark (2011) also found different responses among these species, with Side-blotched Lizards, but not Whiptails, decreasing at Sonoran Desert sites in response to urbanization and habitat fragmentation. Flesch et al. (2017) conducted extensive surveys in the Arizona Sonoran Desert from 1989 to 2013 and found that Side-blotched Lizards increased over time while the other two species decreased, showing that these species respond differently to environmental change. Increases or decreases in density of different lizard species over time may be partially attributable to differences in life history strategy among the species. Side-blotched Lizards show considerable spatial and temporal demographic variation (W. S. Parker & Pianka, 1975; Wilson, 1991; Zani, 2005), with lifespans ranging from four months (Tinkle, 1967, Texas) to over several years (Turner et al., 1970, Nevada; Zani & Stein, 2018, Oregon), and with some populations experiencing annual turnover (Tinkle, 1967). Southern populations generally appear to be shorter-lived, which may make them particularly sensitive to conditions during the short reproductive window during their first—and possibly only—breeding season. Both rainfall and predation have been identified as important sources of mortality for Side-blotched Lizards (W. S. Parker & Pianka, 1975; Wilson, 1991; Zani & Stein, 2018). Additional data on species-specific habitat quality, stressors, and biotic interactions would be necessary to understand what is driving these different responses across the landscape.

We did not see a reduction in Whiptail abundance over time; rather, we saw extensive year-to-year variation. While three out of five sites with historical data showed a trend toward lower contemporary abundance (i.e., declines), this observation is driven almost entirely by low values for this species in 2022, which tended to be a dry year at most sites (Fig. 1). Side-blotched and Zebra-tailed Lizards also tended to show lower abundances in 2022, but the effect was not as large as for Whiptails. We lack historical data for Zebra-tailed Lizard abundance, so we are unable to assess the potential for declines in this species over time. Zebra-tailed Lizards were generally at densities below 1 per ha except for the Mojave and Grapevine sites.

Unbeknownst to us during our field work, Furnas et al. (2019) were also conducting surveys of contemporary lizard populations, which provided an opportunity for the comparison of two different strategies. While we sampled a small number of historical resurvey sites over a span of several years (2015–2022), they surveyed over 200 sites within a single year (2016). Furnas et al. (2019) built more elaborate distance models by incorporating additional hierarchical structure and environmental covariates and used these to extrapolate lizard abundance across the Mojave Desert. We compared our estimates from the seven sites we sampled in 2016 to Furnas et al.'s (2019) model-extrapolated densities from the nearest 1 km^2 cell to our sites. We found a positive correlation between our and Furnas et al.'s (2019)

densities for Side-blotched Lizards, but with a large confidence interval that included zero: Pearson's correlation coefficient = 0.65, 95% CI (-0.2, 0.94). Thus, while there was some overall agreement among the studies, Furnas et al. (2019) predicted much higher densities in two of our three sites where our surveys found that Side-blotched Lizards were extremely rare (Searchlight and Mojave). Such a result is not surprising when looking for correlations among only seven points. Furnas et al. (2019) noted that coarser regional comparisons may be more informative than finer site-scale comparisons. However, given our relatively small number of sites and their distribution across the Mojave, we are unable to make a broader regional comparison with the data at hand. Correlations between the studies for Whiptails and Zebra-tailed Lizards were much weaker, and Furnas et al. (2019) were similarly unable to corroborate their model results for Whiptails in Joshua Tree National Park. They concluded that this was due to differences in activity among the three species, such that Whiptails were less likely to be observed on surveys (i.e., less available for sampling). However, in our surveys we found that Whiptails were detectable at greater distances than Side-blotched Lizards (Fig. S1), which was the opposite of Furnas et al. (2019) and may also contribute to the different estimates from the studies.

What we can take from this comparison is that monitoring efforts likely need to cover both spatial (many sites) and temporal (many visits) variation, and that additional environmental covariates are likely necessary to improve model extrapolation at a fine scale. Despite substantial field efforts of ourselves and Furnas et al. (2019), both studies only estimated abundance for the same three common species, and neither was able to collect enough data to generate reasonable abundance estimates for the other eight flatland desert lizard species. While the distance models used by both studies have the desirable feature of providing abundance estimates without labor-intensive mark-recapture of animals, a drawback is that they require many observations to fit detection functions that underlie abundance estimates. Taxa that occur at low density, or are not easily detected using visual encounter transects, are therefore not good candidates for this approach. High uncertainty between the studies also underscores that the same methods should be used in the same places over time to monitor populations, such that differences in abundance are not confounded with differences in approach.

If we only considered occurrence, then we would conclude that flatland lizard communities have been stable over time despite significant warming and increased human development. Side-blotched Lizards continue to occur everywhere Pianka surveyed them in the 1960s, but the populations are clearly not all doing equally well. Declines

in the status of populations is particularly striking given that Side-blotched Lizards are considered a common and widespread species. If Side-blotched Lizard populations are declining, then it becomes important to determine the fates of populations that were rare initially. Despite the difficulty involved, it is critical to monitor abundance because declines to extirpation can take a long time, and this window provides the best (or only) opportunity for conservation intervention. For example, the high densities of Side-blotched Lizards we observed at some sites suggests potential for resiliency in this species through range shifts or higher elevation refugia (Barrows et al., 2020). Our results also highlight the difficulty of estimating abundance for even the most common desert lizards and indicate that greater effort is needed to track and model these populations. With ongoing warming and development in the Mojave Desert and future habitat projections generally predicting continuing loss or degradation of habitat for Mojave reptiles (Barrows, 2011; Wright et al., 2013), establishing monitoring efforts throughout the desert is critical. Although historical abundance data are limited, it has provided us with a window into the changes experienced by these populations over time, and we hope that our expanded abundance estimates, along with the efforts of Furnas et al. (2019) and others, will provide repeatable baselines for future work.

Supplementary Data

Supplementary data associated with this article can be found online alongside the manuscript.

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SUPPLEMENTARY DATA

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