

CONTRIBUTED PAPER

Genetic and environmental factors associated with survival of a rare songbird in a fragmented urban landscape

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Abstract

The coastal Cactus Wren (*Campylorhynchus brunneicapillus*) persists in small and fragmented populations throughout southern California that are subject to genetic drift and inbreeding. We combined individual banding and resighting data and genotyped individuals at 22 microsatellite loci to assess whether heterozygosity was associated with survival across three regional Cactus Wren populations on conserved lands in Orange and San Diego Counties between 2009 and 2020. Using Cormack-Jolly-Seber models (CJS) to analyze the 5-year capture histories of 528 individual wrens, we found that age class (hatch year or after hatch year) was the strongest predictor of survival. Individual heterozygosity and precipitation also had positive effects on survival, with survival up to 2 times higher in the most heterozygous individuals compared to the least and up to 1.5 times higher in high precipitation years versus drought years. Multi-locus heterozygosity was significantly correlated across loci, suggesting that inbreeding depression is likely driving the association between survival and heterozygosity. Study results support that genetic rescue efforts that reduce inbreeding have the potential to improve fitness and mitigate further loss of genetic variation in managed populations.

KEYWORDS

Cactus Wren, heterozygosity fitness correlations, mark resighting, microsatellites, small-population conservation, southern California

1 | INTRODUCTION

Factors that influence individual survival are important to understand in rare and declining species to inform population and habitat management actions aimed at enhancing population viability. Drivers can include both extrinsic environmental and ecological factors (climate, habitat, food availability, predation, competition) and intrinsic genetic factors (variation and adaptation) as well as their

interactions (Frankham et al., 2017; Schwartz et al., 2007). While management emphasis is often on manipulating extrinsic factors, particularly through habitat restoration and enhancement, there is a growing focus on understanding the role of genetic variation and the potential importance of genetic rescue to counteract inbreeding depression and restore genetic variation to improve adaptive potential (Carlson et al., 2014; Clarke et al., 2024; Frankham, 2015; Weeks et al., 2011; Whiteley et al., 2015).

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Small and isolated populations are vulnerable to erosion of genetic variation through inbreeding (breeding between close relatives) and genetic drift (loss of alleles due to random chance; Frankham, 2005). Inbreeding is an especially pernicious mechanism of genetic erosion in vulnerable populations because it can lead to inbreeding depression, the reduction of fitness, which is predominately caused by the unmasking of recessive deleterious mutations (Charlesworth & Willis, 2009). Reduction of fitness (traits such as survival and productivity) can then reduce population sizes even further, leading to more pervasive inbreeding via a feedback loop known as the extinction vortex (Gilpin & Soulé, 1986). When inbreeding depression is occurring, an individual's multilocus heterozygosity is hypothesized to correlate with fitness traits, such as rate of development, susceptibility to disease, survival, and productivity (Szulkin et al., 2010). Thus, these associations, or heterozygosity-fitness correlations (HFCs), have been used as proxies to evaluate the fitness consequences as heterozygosity declines with increased inbreeding (Szulkin et al., 2010). While the power of HFCs to detect the effect of inbreeding on fitness can depend on the amount of standing variation in a population, the number of markers assessed, as well as the timing of sampling in relation to the population's demographic decline, there is a general consensus that HFCs can be an important metric to monitor, particularly in small and fragmented populations (Grueber et al., 2008). Understanding the fitness impacts of low genetic variation in threatened populations could be critical to informing population management (Clarke et al., 2024; Kerk et al., 2019).

The Cactus Wren (*Campylorhynchus brunneicapillus*) is a non-migratory songbird that nests exclusively in cacti. The species range extends through the deserts of central Mexico through the southwestern USA from Texas to southern California (Figure 1, inset). Although the Cactus Wren has an IUCN (International Union for Conservation of Nature) listing of least concern, at its range edge in coastal southern California, populations are disjunct from the desert interior and restricted to small patches of coastal sage scrub habitat that contain sufficient mature prickly pear (*Opuntia* spp.) and cholla (*Cylindropuntia prolifera*) plants to support nesting. Populations in this portion of the range have been greatly affected by habitat loss and fragmentation (Hamilton et al., 2020) and are recognized as a unique subspecies, *C. brunneicapillus sandiegensis* (Rea & Weaver, 1990), and listed as a Species of Special Concern by the California Department of Fish and Wildlife. Previous population genetic analysis of Cactus Wrens throughout coastal southern California found that they are structured in small local populations, many of which are isolated from

one another by urban development (Barr et al., 2015). In addition, low genetic variation and recent genetic bottlenecks were associated with habitat loss and disturbance from recent and frequent wildfires (Barr et al., 2015). Population monitoring also suggests that environmental extremes, such as longer and more intense periods of drought, reduce reproductive output and abundance in remaining populations. The amount and timing of rainfall, for example, can affect productivity in Cactus Wrens by influencing food availability during nesting, with both extreme drought and extremely wet and cold winter conditions associated with declines in productivity and abundance (Hamilton, 2003, 2004; Kamada, 2008; Kamada & Preston, 2013; Lynn et al., 2022; Preston & Kamada, 2012).

In addition to drought effects, recent monitoring in Orange County populations documented low survival and productivity and high probability of local extinction due to limited dispersal opportunities (Kamada & Preston, 2013). Similarly, monitoring in San Diego County populations found that annual breeding adult population sizes were small (numbering in the low tens of individuals) and were dispersal-limited (Lynn et al., 2022). Further, these populations have lost genetic variation (measured as population-level heterozygosity and allelic richness) over the past decade (Vandergast et al., 2022a). However, the extent to which low genetic diversity impacts individual fitness of Cactus Wrens in small and geographically isolated coastal populations has not been previously investigated.

In this study, we aimed to fill this critical knowledge gap by analyzing individual genetic and survival data collected in two long-term demographic studies of Cactus Wrens spanning 11 years. We modeled the relative effects of individual heterozygosity and variation in rainfall and temperature on apparent survival in focal populations in Orange and San Diego Counties. Results from this work can help inform management by improving our understanding of the relationship between survival and genetic variation in Cactus Wrens, and whether genetic rescue efforts could be warranted to mitigate loss of genetic variability in managed populations.

2 | METHODS

2.1 | Field monitoring and apparent survival estimates

Three regional genetic populations (hereafter regions) were monitored with banding and resighting, as part of long-term monitoring efforts of the Nature Reserve of Orange County and San Diego County Multiple

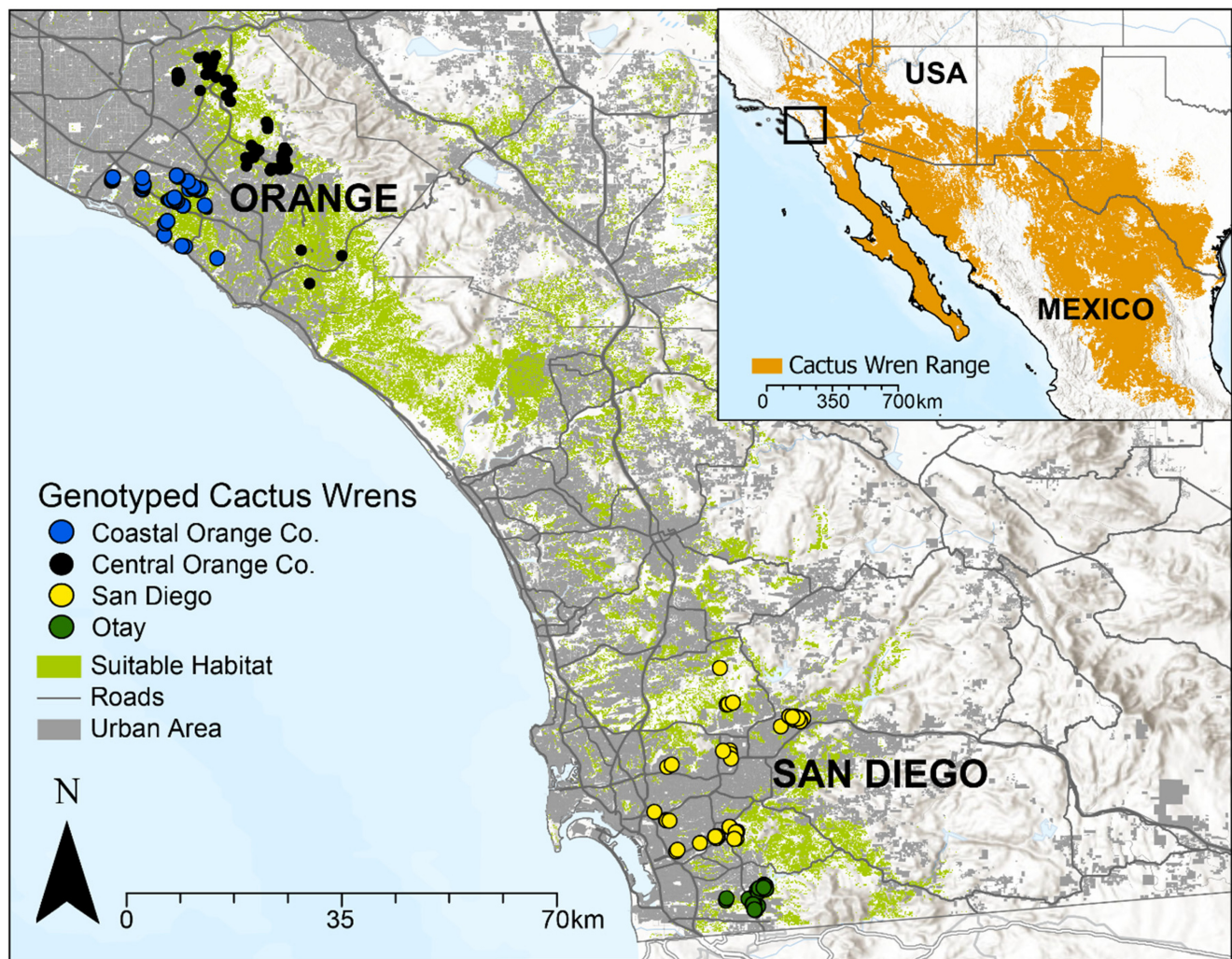


FIGURE 1 Territory locations for genotyped Cactus Wrens (*Campylorhynchus brunneicapillus*) across Orange and San Diego Counties, California, USA. Locations are colored by regional genetic populations. Birds from the Coastal Orange County (blue), San Diego (yellow), and Otay (green) regional populations were followed with mark recapture and were included in the survival analyses. Areas of suitable habitat ($HSI \geq 0.50$ from Preston et al., 2020) are mapped in light green. The inset map shows the location of the southern California sampling area (box), where populations are sparse and disjunct, in relation to the full species range (data from ebird Status and Trends 2023 Mean Abundance; Fink et al., 2024). Base map layers sourced from Esri, TomTom, Garmin, FAO, NOAA, USGS, OpenStreetMap contributors, and the GIS User Community.

Species Conservation Programs. These regional populations were previously found to be genetically distinct from other populations throughout southern California using 22 microsatellite loci in an analysis of genetic structure (see Barr et al., 2015) (Figure 1). The three focal regions included the coastal reserve of Orange County (Orange County Coastal, monitored between 2009 and 2013) and two regions in San Diego County (San Diego and Otay, monitored between 2016 and 2020). Although not concurrent, the sample periods in Orange County and San Diego County each spanned a range of low and high rainfall years. Both studies used similar data collection methods. Adults and fledglings were captured using mist nets and song playback to attract birds to nets.

Captured adults and fledglings and hatchlings from accessible nests were banded with unique combinations of colored leg bands, and a genetic sample (blood or feather) was taken. Banding and sample collection activities were authorized under California Department of Fish and Wildlife Scientific Collection permits 001360 and S-190290006-20062-001, USGS Federal Master Banding Permits 22956 and 22372, and USGS WERC Animal Care and Use Committee's approved protocol 20250307901. Adults and fledglings were aged based on plumage, and sex was assigned to adults based on behavioral cues, including position during copulation, incubation (only females incubate), morphology (females have brood patches, males have cloacal protuberances), or call/song

frequency. Cactus Wrens were resighted and individuals identified based on color-band combinations in monitored territories and surrounding survey plots to detect dispersing individuals. Territories were monitored weekly between February and August in each year of the study. To assess the survival of hatchlings, brood nests were identified by the presence of eggs or nestlings and were checked weekly using either a fiber optic camera or by reaching in to feel for contents to determine the number of eggs, the number and age of nestlings, and whether the young had successfully fledged (nestlings reaching 19 days of age or detected alive outside of the nest). We used resighting data to create a 5-year capture history for each individual and defined “survival” as apparent survival from the banding year to March 1st of the next year and each subsequent year. Additional field data and collection methods can be found in Preston and Kamada (2012) for Orange County and Lynn et al. (2022) for San Diego County.

2.2 | Genetic data collection and heterozygosity estimation

Genetic data were collected from the three regional populations described above, and a fourth, nearby, regional population found in the Orange County central reserve (hereafter Orange County Central; Figure 1; Barr et al., 2015). This population extends throughout the foothills of the Santa Ana Mountains through Marine Corps Base Camp Pendleton in one of the largest contiguous areas of occupied habitat in southern California. Briefly, we extracted genomic DNA from pin feathers, secondary feathers, or blood, and genotyped individuals using two to five multiplex PCRs (polymerase chain reactions) at the previously developed 22 microsatellite loci (Barr et al., 2015). Amplification conditions are further detailed in Barr et al. (2015) and Vandergast et al. (2022a). We scored microsatellites using Genemarker version (v) 3.0.1 and binned using MsatAllele v 1.03 (Alberto, 2009). We standardized allele size calls between these two genetic datasets using a subset of 104 samples genotyped in both studies.

We used the likelihood method of COLONY v 2.0.6.6 (Jones & Wang, 2010) to confirm field observations of parentage and to estimate population allele frequencies in the 2009–2013 Orange County dataset and the 2016–2020 San Diego County dataset separately. We assigned parentage for all genotyped individuals using the following five input files: (1) offspring genotypes, including all genotyped individuals; (2) candidate sire genotypes, including all genotyped field-observed sires; (3) candidate dam genotypes, including all genotyped field-observed

dams; (4) list of field-observed paternal and maternal sibling relationships; and (5) list of excluded candidate parents for each offspring, which included all individuals from the same cohort or younger cohorts (all individuals that were banded as nestlings in the same or subsequent years). We ran COLONY twice, using the following parameter settings: both genders polygamous, inbreeding allowed, long length run, full-likelihood analysis, very high precision probability, weak prior (2.2 males, 2.2 females), unknown and updated allele frequencies, probability of a parent being sampled = 0.5, mismatching for full sibship data set allowed at 4 out of 24 loci. We compared paternity and maternity results of the two COLONY runs, accepting only those parentage assignments that appeared in both runs. We compared genetic parentage assignments with field-observed assignments.

To estimate heterozygosity within individuals, we used the R package GETHET (Coulon, 2010) with allele frequencies inferred from COLONY to calculate four measures of individual heterozygosity for all genotyped individuals: standardized heterozygosity based on the mean observed heterozygosity (H_{sobs}), standardized heterozygosity based on the mean expected heterozygosity (H_{sexp}), homozygosity by locus (HL), and internal relatedness (IR). A sufficient level of variation in inbreeding is needed to detect HFCs. To quantify inbreeding variance, we estimated the extent to which heterozygosity was correlated among loci (g_2 , identity disequilibrium) using the R package inbreedR (Stoffel et al., 2016, $nperm = 1000$, $nboot = 1000$). We estimated the expected squared correlation [$r^2(h,f)$] between heterozygosity (h) and the inbreeding level (f) in inbreedR ($nboot = 1000$), following equation 2 in Stoffel et al. (2016). We conducted these analyses on the subset of birds included in the survival analysis described below ($N = 528$).

2.3 | Weather variables

Total monthly precipitation and monthly minimum and maximum temperature variables were downloaded from PRISM at 4 km resolution (PRISM Climate Group, Oregon State University, <https://prism.oregonstate.edu>, accessed 3 April 2024). These were extracted for each territory location from 2000 through 2021 in ArcGIS. We then calculated the Standardized Precipitation Index (SPI; Guttman, 1998) and Standardized Temperature Index (STI; Fasel, 2015) for each territory ($N = 182$). Precipitation data are positive and non-normal; therefore, SPI is derived by fitting observed data to an appropriate distribution (e.g., gamma) and then transforming the fitted values to a normal distribution. SPI is calculated for

different timescales and interpreted as the number of standard deviations by which an observed value differs from the long-term mean at that timescale. The STI was calculated using a similar approach to SPI, but because it is appropriate to fit temperature data to a normal distribution, it is calculated by transforming the observed values into standard deviations from the median of a standardized normal distribution. We calculated SPI based on a bioyear from July 1 of the year before the breeding/monitoring season to June 30 of the breeding/monitoring season. We calculated two measures of STI, each at 3-month timescales, to evaluate the influence of hot and cold periods on survival. These included the mean monthly maximum temperatures during the three-month period following breeding (July, August, September; STI_{max}) and the mean monthly minimum temperatures in a three-month winter period following breeding (December, January, February; STI_{min}). These seasonal highs and lows were hypothesized to capture potentially important temperature extremes experienced by Cactus Wrens. We used the packages SPEI (Beguería et al., 2017) and STI (Fasel, 2015) in R (R Core Development Team, 2022) to calculate SPI and STI, respectively.

2.4 | Data analysis

Age class and weather have been previously associated with both survival and productivity in Cactus Wrens (Lynn et al., 2022; Preston & Kamada, 2012). Therefore, we structured our analyses to first explore these key variables and then to model sets of related variables in a step-wise fashion to arrive at final model sets that included heterozygosity. First, we conducted exploratory analyses of patterns of spatial variation in genetic and environmental covariates. We then modeled the relationship of apparent survival with “base” variables (age class, region, time; defined in Table 1), with precipitation and temperature variables added to any base variables found to be important; and then finally with heterozygosity, including factors of high importance in the base and climate models.

2.4.1 | Differences in overall heterozygosity among territories and regions

We used linear mixed effects models (LMM) to analyze differences in heterozygosity among territories and regions, where regions corresponded to previously defined genetic populations (Orange County Coastal, Orange County Central, San Diego, Otay; Barr et al., 2015). We found very strong correlations ($r \geq 0.953$) among the four

TABLE 1 Definitions of the explanatory variables included in survival models and the model groups within which they were included.

Variable	Definition	Model group
Age class	Hatch year, after hatch year	Base, combined
Time	Standardized study year (1–5); Orange County time 1 = 2009; San Diego County time 1 = 2016	Base
Region	Previously defined regional genetic populations: Orange County coastal, San Diego, Otay	Base
SPI ₁	Standardized precipitation index of the bioyear (July 1st, prior to breeding/monitoring season—June 30 of breeding/monitoring season)	Precipitation, combined
LagSPI	Standardized precipitation of the previous bioyear	Precipitation
STI _{max3}	Mean monthly maximum temperatures during the 3-month period following banding/sighting (July, August, September)	Temperature
STI _{min3}	The mean monthly minimum temperatures in a 3-month winter period following initial banding/sighting (December, January, February)	Temperature
H _{sexp}	Standardized individual heterozygosity based on the mean expected heterozygosity by county	Combined

measures of multilocus heterozygosity (H_{sobs} , H_{sexp} , HL, IR); therefore, we selected H_{sexp} as the response variable for this and all subsequent models. Region was specified as the fixed factor and territory as a random effect. We conducted one analysis using all genotyped birds ($N = 818$; four regional populations) and another using only those birds monitored with mark-recapture data ($N = 528$; three regional populations). We plotted regional averages of H_{sexp} over time to further examine temporal trends.

2.4.2 | Variation in precipitation among regions and counties

We used Multivariate Autoregressive State-Space (MARSS) models to evaluate the degree to which precipitation (SPI) varied within and among Orange and San Diego County territories. State-space models are flexible

hierarchical time series models where a state process model is linked to an observation process model (Hampton et al., 2013; Holmes et al., 2012). The time series do not need to be stationary, time periods can differ, and partitioning the state and observation variability can reduce sampling error bias (De Valpine & Hastings, 2002). Potential relationships (covariance) among time series can be explicitly modeled, parameters are estimated by maximum likelihood, and models can be ranked and compared with information-theoretic statistics, such as the bias-corrected version of Akaike's information criterion (AICc; Holmes et al., 2012).

The yearly precipitation time series were grouped together at two scales: (1) territories within regions (Orange County Coastal, San Diego, and Otay); and (2) territories within counties (Orange County and San Diego County). We compared five models: (1) similar precipitation amounts and variability across counties and regions; (2) similar precipitation amounts but different variability between the counties; (3) different amounts and variability in precipitation between the counties; (4) similar precipitation amounts but different variability among the regions; and (5) different precipitation amounts and variability among the regions. Models were compared with ΔAICc and AICc weights ($w\text{AICc}$) (Burnham & Anderson, 2004). The package MARSS in R (Holmes et al., 2014) was used to derive parameter estimates and compare the five models.

2.4.3 | Relationship of survival with precipitation, temperature, and heterozygosity

We used Cormack-Jolly-Seber models (CJS) to analyze the relationship of survival with base factors (age class, region, time), weather (precipitation and temperature), and heterozygosity (H_{sexp} ; Table 2). Precipitation included SPI at the 1-bioyear scale (hereafter, SPI_1) and a one-year lag of SPI_1 (LagSPI_1), representing the potential influence of rainfall in the previous bioyear. Temperature variables included STImax_3 and STImin_3 . Only birds

monitored in all 5 years in each county were used in the analyses ($N = 528$; Table 1). These comprised birds initially banded in two age classes: during their first year (hatch year birds [HY]; $N = 465$) and those banded after hatch year (AHY; $N = 63$). Because birds were banded in different years in the two counties, we use time in the base models instead of year (Table 1).

We used the RMark package in R (Laake, 2013) to estimate probabilities of apparent survival and recapture. The analysis consisted of three steps. First, we compared eight models with different combinations of variation in survival of HY and AHY birds by time, age class, and/or region (base model group; Table 2). The purpose of this step was to evaluate the magnitude of difference in survival between HY and AHY birds to determine whether they could be pooled or kept separate in subsequent models. We note that while CJS models can analyze age and cohort effects, birds first banded as adults (AHY birds) were of unknown age, and Orange and San Diego birds were from different time periods. Thus, the inclusion of those effects would not have made sense. Important factors in the base model (in this case "age class") were included in subsequent model groups.

Cactus Wren reproductive success and survival are influenced by weather patterns (Lynn et al., 2022), and weather patterns could potentially work additively or interactively with heterozygosity. Therefore, our second step consisted of comparing models where survival was influenced by: (1) precipitation and age class; and (2) temperature and age class. The final step compared the best supported model from the weather group to models with additive and interactive effects of weather, heterozygosity, and age class. Because of similar levels of support between some of the models in this group (see section 3), we defined a 95% confidence model set and used model averaging (Burnham & Anderson, 2004) to derive final parameter estimates and predicted values of survival for the HY and AHY age classes. The same territories were visited from year to year and a very large proportion of banded birds were seen in the sampling periods; therefore, we specified recapture probability to be constant in

County	Region	Hatch year	After hatch year	Total
Orange	Coastal	141 [21]	33	174
San Diego	Otay	160 [35]	5	165
San Diego	San Diego	164 [46]	25	189
Total		465 [102]	63	528

Note: The study was conducted from 2009 through 2013 in Orange County and 2016 through 2020 in San Diego County. Most birds were banded in their hatch year (numbers in brackets include the subset of hatch year birds that were observed in subsequent years as adults). A smaller set (63) of birds were initially banded as adults (after hatch year).

TABLE 2 Sample sizes of Cactus Wrens in a mark-recapture study conducted in three regions in California, USA.

all models. Models were compared with ΔAICc and wAICc .

3 | RESULTS

3.1 | Parentage and individual heterozygosity

In total, we genotyped 818 individuals across 182 territories throughout the study area (Figure 1; raw data available in Vandergast et al., 2022b). In all sampled nests where one or both field-observed parents were also genotyped, field-observed parentage was confirmed by the genetic assignments. Further, there were no nests with more than two genetically assigned parents. Therefore, we found no evidence of extra-pair matings, filling an important gap in

reported behavioral information for Cactus Wrens (Hamilton et al., 2020). Of the genotyped birds, 528 were followed with mark recapture and were included in the survival analyses. For this subset of birds, identity disequilibrium was positive ($N = 528$ birds: $g_2 = 0.0122$, $\text{se} = 0.0028$, 1-sided $p \leq .001$). The expected squared correlation (r^2) between heterozygosity and inbreeding was also positive ($r^2 = 0.36$; 95% CIs 0.25–0.45, based on 1000 bootstraps over individuals).

Raw individual heterozygosity values (calculated as the proportion of heterozygous loci) ranged from 0.09 to 0.95 (Data D1 Supporting Information). After standardization, individual heterozygosity (H_{sexp}) in the Otay region was higher than in the other regions for all genotyped birds ($N = 818$; Figure 2a), as well as the subset followed with mark-recapture ($N = 528$; Figure 2c). In contrast, the distribution of random effects indicated territories had similar

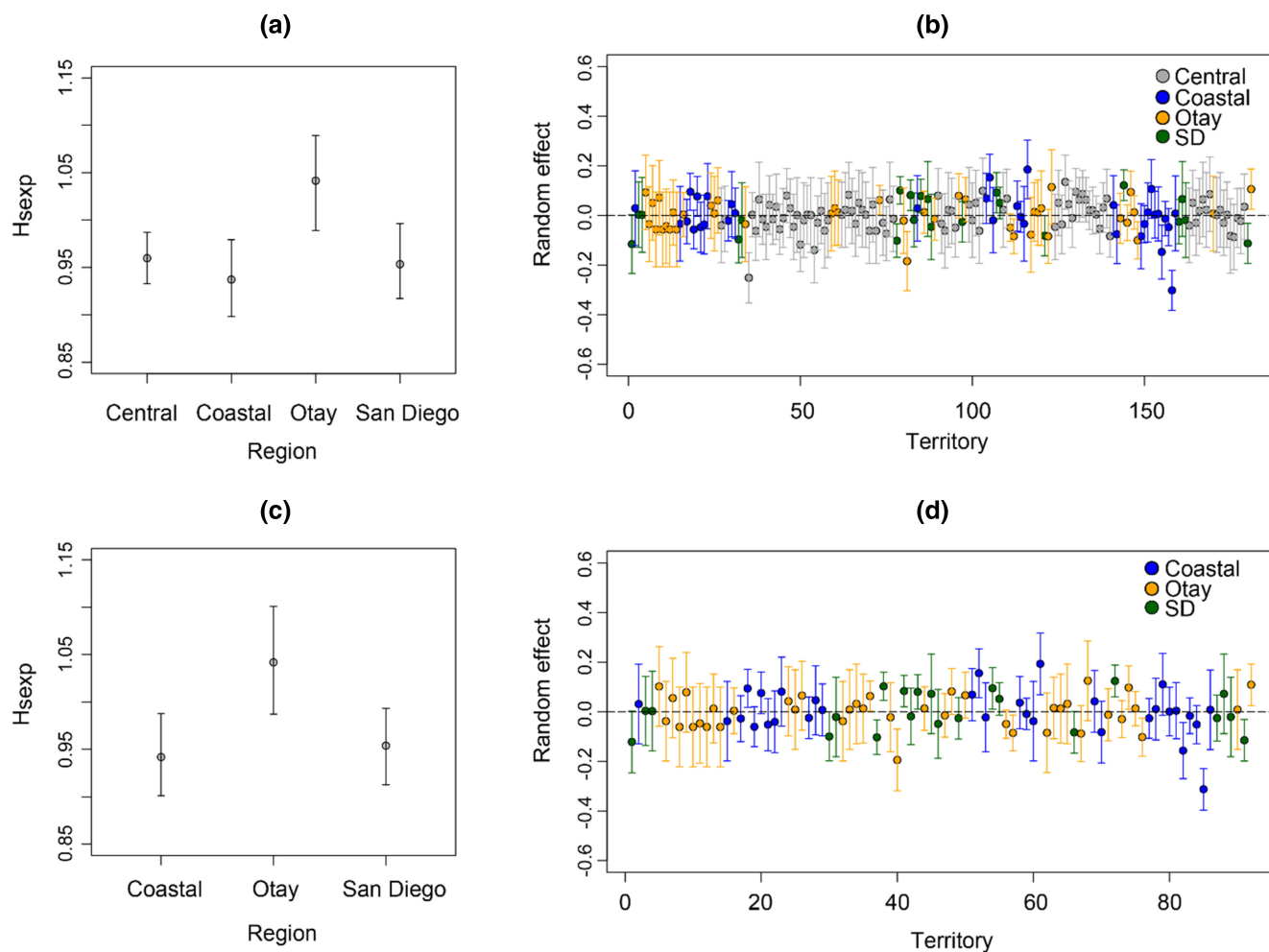


FIGURE 2 (a) Levels of standardized heterozygosity ($H_{\text{sexp}} \pm 95\% \text{ CI}$) in all genotyped Cactus Wrens ($N = 818$) and (b) random effects for H_{sexp} from 182 territories across four regions in Orange (Central, Coastal) and San Diego (Otay, San Diego) counties, California, USA. (c) Levels of standardized heterozygosity ($H_{\text{sexp}} \pm 95\% \text{ CI}$) in Cactus Wrens ($N = 528$) followed by mark recapture and (d) random effects for H_{sexp} from 92 territories across three of the four regions (Coastal, Otay, San Diego). Cactus Wrens were captured from 2009 through 2013 in Orange County and from 2016 through 2020 in San Diego County.

levels of variability within and among the regions (Figure 2b,d). Further examination of heterozygosity by annual cohorts showed that heterozygosity significantly declined over the monitoring period in the Otay regional population, eventually reaching similar levels to the San Diego regional population (Figure S1; Pearson $r = -0.244$; $t = -3.1645$, $df = 158$, p -value $< .0019$).

3.2 | Variation in precipitation among regions and counties

The model with similar amounts and variability in SPI_1 across counties and regions had full support ($wAICc = 1$, $\Delta AICc = 157$ for the second ranked model; Table S1). However, while the amount and variability in SPI_1 across counties were similar, the form of their dynamics differed over the different capture periods. Monitoring of Cactus Wrens in Orange County occurred over a 5-year period when precipitation increased from 2009 to a peak in 2011, then declined through 2013 (Figure 3). In San Diego County, SPI_1 declined sharply from a peak in 2017 to a low in 2018, followed by a rapid increase to another peak in 2019 and then a slight decline in 2020 (Figure 3).

3.3 | Relationship of survival with precipitation, temperature, and heterozygosity

The base models with influences of age class and region on survival had complete support compared to the other five

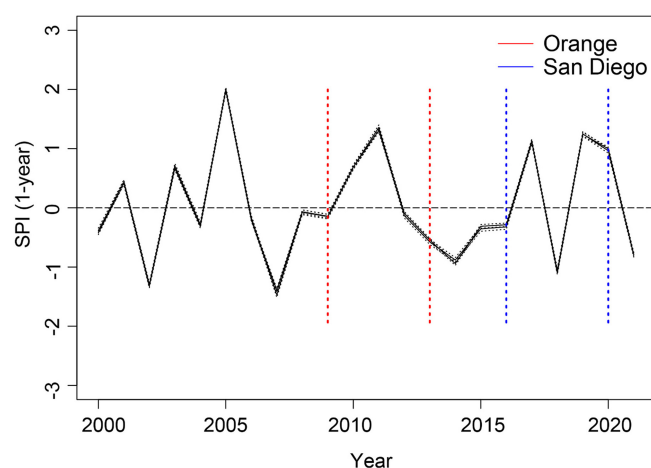


FIGURE 3 Dynamics in the standardized precipitation index ($SPI_1 \pm 95\%$ CI) at a 1-year timescale over a 22-year period in Orange and San Diego Counties, California, USA. Dashed vertical lines mark the 5-year periods when mark-recapture monitoring of California Cactus Wren survival was conducted in each county (red = Orange County, blue = San Diego County).

base models (Table 3; $wAICc = 1$). The age class model had almost $5\times$ more support than the age class + region model and almost $7\times$ more support than the age class $\times$ region model. In addition, the 95% CIs for the region parameters overlapped zero and there was wide overlap in the CIs of the survival estimates between the three regions (Table S2). Therefore, based on parsimony we selected the age class model as being best supported. Based on that model, survival of AHY birds ($\Phi = 0.685$, $SE = 0.048$, $CI = 0.584-0.771$) was almost double that of HY birds ($\Phi = 0.359$, $SE = 0.024$, $CI = 0.312-0.409$). Capture probability in the base model was very high ($p = 0.843$, $SE = 0.042$, 95% $CI = 0.743-0.909$).

Preliminary models with climate variables revealed associations between survival and precipitation. Precipitation models that included SPI_1 accounted for 90% of model support (Table 3). Additionally, the estimates of survival showed no meaningful variation with $LagSPI_1$ (Figure S2 and Table S3). Therefore, the model with the effect of just SPI_1 was selected as the most statistically parsimonious and biologically relevant. The temperature models with individual effects of ST_{Imax} and ST_{Imin} had similar levels of support and comprised $>56\%$ of cumulative $wAICc$ (Table 3). However, the best supported model (46% of cumulative $wAICc$) contained only age class. Further, survival estimates did not vary with temperature (Figure S3 and Table S4). Based on these results, ST_{Imax} and ST_{Imin} were not included in any other models.

Based on these preliminary modeling results, final combined models included age class, SPI_1 , and H_{sexp} . The two models with the additive and interactive effects of SPI_1 and H_{sexp} comprised 72% of the cumulative $wAICc$ (Table 3). Models with individual effects of SPI_1 and H_{sexp} comprised an additional 22% of support (Table 3); together these four models made up the 95% confidence set for model averaging (Table S5). Parameter estimates suggested that H_{sexp} had a stronger positive effect on survival than precipitation, but it was not as strong of a predictor as age class (Table S5). While the lower range of the 95% CIs of H_{sexp} overlapped zero, those of the 90% CIs did not in the models included in the 95% confidence set (Table S5). The relationship between survival and H_{sexp} was positive for HY and AHY birds (Figure 4a). In HY birds, survival was $2\times$ greater in birds with the highest levels of H_{sexp} compared to those with low levels of H_{sexp} . Survival in AHY birds was $1.6\times$ greater in those with the highest levels of H_{sexp} compared to those with low levels of H_{sexp} . There was a moderate amount of overlap in CIs of HY and AHY birds at low levels of H_{sexp} (Figure 4a). Survival also had a clear positive relationship with SPI_1 ; it was $1.5\times$ greater for HY birds at high SPI_1 levels than low

TABLE 3 Model selection statistics for Cormack-Jolly-Seber mark-recapture models of the relationship between survival of Cactus Wrens and geographic location (Region), age class (hatch year or after hatch year), precipitation, temperature and heterozygosity (H_{sexp}).

Model	AICc	ΔAICc	wAICc	Cum wAICc	Deviance	Pars
Base models						
Age class	884.1	0.0	0.736	0.736	160.7	3
Age class + region	887.2	3.1	0.156	0.892	159.7	5
Age class $\times$ region	887.9	3.8	0.108	1.000	156.4	7
Time $\times$ region	902.7	18.6	0.000		158.8	13
Time	909.6	25.5	0.000		182.1	5
Time + region	910.9	26.8	0.000		179.4	7
Region	918.7	34.6	0.000		193.3	4
Null	918.8	34.8	0.000		197.5	2
Precipitation models						
SPI_1 + age class	879.7	0.0	0.590	0.590	871.6	4
SPI_1 + Lag SPI_1 + age class	881.7	2.0	0.216	0.806	871.6	5
$\text{SPI}_1 \times \text{LagSPI}_1$ + age class	883.4	3.7	0.094	0.900	871.2	6
Age class	884.1	4.4	0.067	0.967	160.7	3
Lag SPI_1 + age class	885.4	5.7	0.034	1.001	877.4	4
Temperature models						
Age class	884.1	0.0	0.436	0.436	160.7	3
STImax + age class	885.3	1.2	0.240	0.676	877.2	4
STImin + age class	886.0	1.9	0.168	0.844	877.9	4
STImax + STImin + age class	887.3	3.2	0.088	0.932	877.2	5
STImax*STImin + age class	887.8	3.7	0.068	1.000	875.6	6
Combined models						
H_{sexp} + SPI_1 + age class	878.0	0.0	0.402	0.402	867.9	5
H_{sexp} * SPI_1 + age class	878.5	0.5	0.320	0.722	866.3	6
SPI_1 + age class	879.7	1.7	0.172	0.894	871.6	4
H_{sexp} + age class	882.3	4.3	0.046	0.940	874.3	4
$H_{\text{sexp}} \times \text{age class}$	883.9	5.9	0.021	0.961	873.8	5
$H_{\text{sexp}} \times \text{SPI}_1 \times \text{age class}$	884.0	6.0	0.020	0.981	865.7	9
Age class	884.1	6.1	0.019	1.000	160.7	3
H_{sexp}	918.4	40.4	0.000	1.000	912.3	3

Note: The study was conducted from 2009 through 2013 in one region in Orange County and 2016 through 2020 in two regions in San Diego County, California, USA. Time represents the years (1–5) of study in the respective counties. SPI_1 = the standardized precipitation index at a 1-year timescale. $\text{STI}_{\text{max}3}$ = the standardized temperature index in the 3 months following breeding (June, July, August). $\text{STI}_{\text{min}3}$ = standardized temperature index in the three winter months after breeding (December, January, February). AICc is the bias-corrected Akaike information criterion, wAICc is the AICc weight, Deviance is the model deviance, and Pars is the number of parameters in the model.

levels, and $1.2 \times$ greater for AHY birds at high compared to low SPI_1 levels (Figure 4b and Table S4).

4 | DISCUSSION

The Cactus Wren has declined dramatically across coastal southern California over the past 50 years or more in response to habitat loss from urbanization and

wildfires (Hamilton et al., 2020; Preston et al., 2025; Rea & Weaver, 1990). Multiple ecological and genetic studies have emphasized the sensitivity of Cactus Wrens to habitat fragmentation, which has resulted in smaller population sizes, erosion of genetic variation, and local extirpation (Barr et al., 2015; Crooks et al., 2001; Lynn et al., 2022; Preston & Kamada, 2012; Vandergast et al., 2022a). Here we sought to measure fitness consequences of low genetic diversity, chiefly to understand

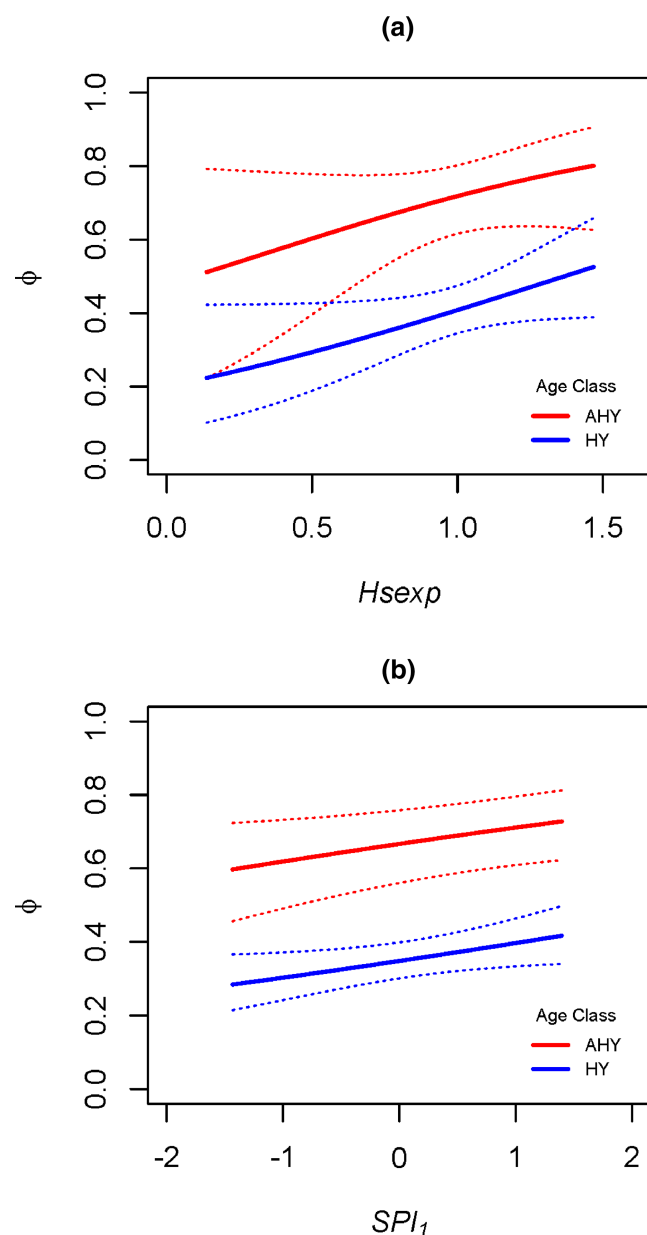


FIGURE 4 Relationship of survival ($\phi \pm 95\%$ CI) of Cactus Wrens with: (a) standardized heterozygosity (H_{sexp}), and (b) the 1-year standardized precipitation index (SPI_1) for hatch year (blue) and after hatch year (red) birds. Cactus Wrens were captured from 2009 through 2013 in Orange County and from 2016 through 2020 in San Diego County, California, USA. Survival estimates and 95% CIs were derived by model averaging a 95% confidence set of the top four candidate models that included the additive and interactive effects of heterozygosity, precipitation, and age class on survival (see Table 3).

whether inbreeding is linked to reduced survival. Indeed, we found that apparent survival was strongly associated with age class, interannual variation in precipitation (as previously reported), and individual heterozygosity, which had a positive effect on survival.

Associations between fitness and heterozygosity in neutral microsatellite markers, the type of marker used in our study, are likely to reflect demographic processes acting at the whole genome level such as breeding among close relatives, genetic drift, and bottlenecks, which can all contribute to identity disequilibrium (Balloux et al., 2004; Szulkin et al., 2010). Alternative potential causes include overdominance (greater fitness advantage at the surveyed markers) or selection on closely linked loci, but these are less likely to affect all markers. We found significant covariation in heterozygosity across markers (e.g., identity disequilibrium) and a significant relationship between heterozygosity and inbreeding. Several HFC studies have noted weak or intermittently detectable signals in wild populations, suggesting HFCs are dependent on specific environmental contexts following population declines, bottlenecks, or mating among close relatives, and require sufficient variance in inbreeding in the system to be detectable (Kardos et al., 2014; Szulkin et al., 2010). For example, in the Blue Tit (*Cyanistes caeruleus*), the strength of the association between heterozygosity and recruitment was stronger under harsher environmental conditions and varied over time (Ferrer et al., 2016). In addition, HFCs may be weaker in studies with smaller numbers of markers (Balloux et al., 2004; Kardos et al., 2014). Some of the early samples obtained for this study consisted only of body feathers, which did not yield enough DNA to attempt whole genome sequencing or reduced representation genomic sequencing methods. Future collection efforts targeting higher quality blood samples could allow for genetic monitoring with a larger set of genome-wide single nucleotide polymorphisms (SNPs) which may provide more power to detect associations. Nonetheless, the associations that we found with microsatellite markers are still compelling.

In Cactus Wrens, differences in individual heterozygosity were structured mostly at the territory scale, with most variation partitioned among territories. While Otay had higher levels of heterozygosity than the other two regions, this appeared to be transient. Heterozygosity declined in cohorts over time in the Otay regional population, eventually reaching similar levels to San Diego. This decline in heterozygosity occurred even though Otay recovered slightly during the 2015–2019 period of study, increasing from 14 pairs in 2014 to 34 pairs in 2018, but declining again to 24 pairs in 2019 (Lynn et al., 2022). The estimated effective population size (N_e) of this regional population was very small (95% CIs = 21.7–30.9; Vandergast et al., 2022a), as were the other two regional populations included in this study (San Diego N_e 95% CIs = 14.8–23.5, Vandergast et al., 2022a; Orange County Coastal N_e 95% CIs = 12.9–24.1, Barr et al., 2015).

Similarly small ($N_e = 50$) modeled populations of Cactus Wrens continued to lose genetic variation without dispersal and gene flow from other populations (Vandergast et al., 2022a).

A positive relationship between heterozygosity and survival indicates that efforts to reduce inbreeding and improve genetic variation within sites could facilitate local population growth and recovery. In Cactus Wrens, it appears that relatively small and isolated local populations coupled with intermittent declines in population size driven by drought and habitat degradation are associated with inbreeding depression (Preston et al., 2025). Generally, local populations of Cactus Wrens are too small to build and retain genetic variation over time without sufficient dispersal and gene flow among them, and genetic variation has measurably declined in some regional populations in San Diego County over just a few generations (Vandergast et al., 2022a).

Coupling ongoing habitat restoration efforts with translocations for genetic rescue could be useful to restore genetic variation within populations (Frankham, 1996). Habitat restoration has been shown to improve local conditions and increase available territories for Cactus Wrens (Lynn et al., 2022), thus supporting larger populations. Improving foraging habitat can also lead to increased productivity. Removal of non-native grasses appears to have a positive effect for Cactus Wrens, by opening more bare ground for foraging (Lynn et al., 2022). Both reducing grasses and forbs and increasing cactus cover for nesting habitat may have contributed to the observed growth in the Otay regional population and other locations throughout San Diego County (Lynn et al., 2022; Preston et al., 2025). However, cacti are slow growing, so in areas where cactus restoration is needed to increase nesting habitat, this process could take many years or decades. In the meantime, translocating small numbers of birds among remaining fragmented populations may be beneficial to provide genetic rescue (Frankham, 2015).

Generally, genetic rescue increases heterozygosity and fitness across animal taxa (reviewed in Clarke et al., 2024). Previous simulations based on the Cactus Wren populations studied here suggested that the successful integration of one translocated individual per generation would markedly increase heterozygosity, and successful translocations of 10% of the populations would increase heterozygosity to the levels expected in a pan-mictic population of the same size as all local populations combined (Vandergast et al., 2022a). Next steps in restoration efforts could include pilot studies to determine the feasibility and empirical genetic and fitness outcomes of translocation among regional sites (Vandergast et al., 2022a).

The success of avian translocations can depend on many factors, with animal behavior (including dispersal and movement, social interactions, and foraging behaviors) often cited as the greatest challenge to successful conservation translocations (Berger-Tal et al., 2020). Age of translocated individuals may also impact overall success, but the direction of the effect (whether older or younger birds fare better) can vary substantially among species and systems (Miller et al., 2024). Translocation of Cactus Wrens has already been successfully accomplished in two small pilot studies in which salvaged birds from sites slated for development in central Orange County were moved to coastal Orange County (Kamada et al., 2014). Results of these pilots suggested that translocated adults integrated more readily into the recipient breeding populations than translocated juveniles, with 7 of 12 adults but only 1 of 7 juveniles observed breeding in follow-up surveys (Kamada et al., 2014; Kamada & Mitrovich, 2006). While translocation of live wrens is warranted in cases of salvage, when considering translocations among protected populations, egg swapping may reduce overall impacts and costs, for example, by avoiding the removal of breeding adults from donor populations, reducing the chances of introducing disease and parasites, allowing for learning of site-appropriate foraging and social behaviors, and eliminating the need for supplemental feeding and other expenses associated with introductions of live birds (Kamada & Preston, 2013; Kamada et al., 2014; generally reviewed in Berger-Tal et al., 2020). Successful translocation through egg swaps and cross-fostering has been reported in other avian species (reviewed in Jones, 2004; Spatz et al., 2023). For example, cross-fostering of Red-Cockaded Woodpecker (*Picoides borealis*) nestlings resulted in similar fledging rates as non-fostered nestlings (Wallace & Buchholz, 2001), and relatively high hatching and fledging rates were reported in egg swaps in the Laysan Albatross (*Phoebastria immutabilis*; VanderWerf et al., 2024).

Another important factor in genetic rescue is whether fitness benefits can be sustained over time. One-time or short-duration translocation efforts may have limited benefit after they are over, particularly if the recipient populations remain small and isolated, or breeding success is highly skewed toward a small proportion of individuals (Bell et al., 2019; Robinson et al., 2021). For example, evaluation of an augmented population of the Aotearoa New Zealand Hihi (*Notiomystis cincta*) found higher fitness in individuals with more immigrant ancestry in the first generation of offspring, but that this effect weakened in the second generation and onward (Nichols et al., 2024). Similarly, in Prairie Chickens (*Tympanuchus cupido pinnatus*) translocation immediately improved population fitness, but long-term demographic recovery

was eventually hampered by limitations in available habitat (Bouzat et al., 2009). Findings such as these underscore the importance of sustaining translocation and post-translocation monitoring while also pursuing habitat restoration efforts to support expanding and connecting existing wild populations to retain more genetic variation (Frankham, 1996).

5 | CONCLUSIONS

While age class and precipitation remain strong investigated determinants of survival in Cactus Wrens, this study is the first to quantify links between genetic diversity and survival in Cactus Wrens, likely driven by inbreeding. Precipitation can vary dramatically inter-annually in southern California (Du et al., 2021), and this variability is projected to become even more pronounced with continued climate forcing (Swain et al., 2018). Prolonged or more frequent drought may compound loss of genetic diversity and inbreeding in already small populations, which together could negatively impact Cactus Wren populations. Our results suggest that some populations of Cactus Wrens have experienced inbreeding depression, underscoring the importance of continued management actions aimed at increasing local population size, stability, and connectivity to preserve genetic diversity and improve survival.

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DATA AVAILABILITY STATEMENT

Data are available in a U.S. Geological Survey data release, <https://doi.org/10.5066/P92A0B0P>.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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