Genetic and ecological evidence of long-term translocation success of the federally endangered Stephens' kangaroo rat

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Abstract
The efficacy of translocation as a method for conserving species in peril has not been fully evaluated. Post-release monitoring rarely involves long-term assessments and initial success metrics may not translate to population viability. In particular, genetic factors may play a critical role in fitness following release as founder effect, genetic drift, inbreeding depression and outbreeding depression can influence extinction risk. As part of a multi-year recovery effort, we translocated populations of the endangered Stephens' kangaroo rat (Dipodomys stephensi; SKR), in order to restore population connectivity. Here we evaluate the success of the translocation efforts through long-term population estimation and genetic analyses. We conducted post-release assessments for 9 years, and used Bayesian clustering analysis and principal components analysis (PCA) of 24 microsatellite markers developed for this species to assess genetic admixture between source and translocated populations. Demographic results indicate long-term translocation success, as evidenced by founder survival and establishment, and population growth and regulation. Genetic results show admixture at the release site between genetically discrete source populations, provide definitive evidence that translocated individuals, not immigrants, produced offspring at the release site, that these offspring successfully reproduced and that even with moderate to great genetic differentiation of source populations, outbreeding depression was not detected. Despite the historical failure of heteromyid translocation efforts, our long-term study illustrates how the development of species-specific best practices led to an effective strategy for SKR recovery. More broadly, our results suggest efforts that use a systematic hypothesis-testing framework alongside long-term monitoring offer great promise in improving translocation outcomes.

KEYWORDS
Bayesian clustering analysis, long-term success, parentage analysis, PCA clustering analysis, population estimation, recovery, Stephens' kangaroo rat, translocation

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1 | INTRODUCTION

Conservation translocation is a strategy for relocating wild animals from one site to another to create, reestablish, or augment wild populations for the purpose of species recovery. Over the last 25 years, there has been an exponential increase in translocations used for conservation in response to changes in land use practices that have resulted in degradation, fragmentation, or complete habitat loss (Armstrong & Seddon, 2008; Seddon, Armstrong, & Maloney, 2007). For species with low mobility, fragmentation means restricted dispersal, reduced probability of recolonization, and loss of genetic diversity that can result in genetic differentiation between populations through genetic drift, and high risk of extirpation (Newman & Pinson, 1997). In fragmented landscapes, translocation may serve as a surrogate for natural dispersal, and thus, is a necessary tool in metapopulation expansion and management towards species recovery (IUCN, 2013).

While the ultimate goal of translocation is to establish a viable population without continued intervention, long-term post-release monitoring and release population assessments are rarely conducted (Seddon, 1999; Seddon et al., 2007; but see recovery program for the black-footed ferret, Mustela nigripes; Dobson & Lyles, 2000). Most programs use surveys following release to measure translocation success through short-term survival or reproductive success. Yet, this approach is not sufficient to evaluate the efficacy of conservation translocation for recovery (Brichieri-Colombi & Moehrensclager, 2016; Taylor et al., 2017). Post-release surveys cannot distinguish between reproductive fitness of translocated founders and conspecifics that immigrate to the release site. Moreover, initial success estimates from the settlement and establishment phases may not predict a viable population over, initial success estimates from the settlement and establishment phases may not predict a viable population without continued intervention, long-term post-release monitoring and release population assessments are rarely conducted (Seddon, 1999; Seddon et al., 2007; but see recovery program for the black-footed ferret, Mustela nigripes; Dobson & Lyles, 2000). Most programs use surveys following release to measure translocation success through short-term survival or reproductive success. Yet, this approach is not sufficient to evaluate the efficacy of conservation translocation for recovery (Brichieri-Colombi & Moehrensclager, 2016; Taylor et al., 2017). Post-release surveys cannot distinguish between reproductive fitness of translocated founders and conspecifics that immigrate to the release site. Moreover, initial success estimates from the settlement and establishment phases may not predict a viable population (Bateson et al., 2014; Mulder et al., 2017; Wolf, Garland Jr., & Griffith, 1998). Tracking genetics following release allows for the distinction between translocation success and recruitment to the release site (Greene, Gore, & Austin, 2017), while spatially explicit demographic modeling allows for assessment of long-term population trends (Royle, Chandler, Sollmann, & Gardner, 2013).

It is widely accepted that a key component of ensuring the long-term viability of managed populations is the maintenance of genetic diversity. Population fragments with limited gene flow can become genetically differentiated through random effects of genetic drift and fixation of alleles due to inbreeding, resulting in decreased fitness (Frankham, 2010). Genetic factors are important to consider when establishing new populations as inbreeding and outbreeding depression, genetic erosion, and loss of genetic diversity can have significant impacts on time to extinction (Brook, Tonkyn, O’Grady, & Frankham, 2002; Frankham, 2010; O’Grady et al., 2006; Schwartz, Luikart, & Waples, 2007). In order to address issues of genetic diversity in translocations and reduce the probability of inbreeding depression in the release population, wildlife managers often select founders from multiple source sites. The genetic composition of the founders can influence the persistence of the release population through variation in fitness among the founding groups, maintenance of genetic diversity and outbreeding depression (DeMay, Becker, Rachlow, & Waits, 2017). Numerous studies have characterized genetic diversity of populations following reintroductions, based on changes in allele frequency following release. Fewer studies have examined degree of admixture or interbreeding of founders relevant for conservation management (Williams & Scribner, 2010). Translocations implemented using multiple source populations can provide valuable insight into relationships between demographic characteristics of founders, genetic and demographic measures of release success (Williams & Scribner, 2010), and reveal evidence of mate-choice or outbreeding depression.

Stephens’ kangaroo rat (SKR, Dipodomys stephensi) is a nocturnal granivorous heteromyid rodent native to forb-dominated open grasslands and sparse coastal sage scrub in Riverside and San Diego Counties, California, USA (USFWS, 1997). Like other kangaroo rats, Stephens’ kangaroo rat is considered a keystone species, as its soil disturbance and seed-caching activities significantly affect plant community structure (Brock & Kelt, 2003; Goldingay, Kelly, & Williams, 1997). In 1971, the SKR was listed as threatened under the California Endangered Species Act, and in 1988 the species was recognized as endangered by the U.S. Fish and Wildlife Service (USFWS, 1997). The current imperilment of the SKR is primarily due to the loss of habitat associated with suburban sprawl, conversion of land for agriculture, and the encroachment of invasive grasses (USFWS, 1997). Secondarily, the species has an extremely small range (Bleich, 1977). It is thought that SKR is particularly vulnerable to habitat fragmentation because both juveniles and adults have limited dispersal distances (Price, Kelly, & Goldingay, 1994). While one individual was documented to move 1.04 km, the maximum mean movement for all age and sex categories was substantially less (X = 61.5 m; Price et al., 1994). A spatially explicit metapopulation model for this species indicated that corridors connecting suitable habitat patches should significantly increase persistence (Price & Gilpin, 1996). To date no empirical data have confirmed the role of connectivity in SKR population persistence, but the species has been documented to persist at extremely low population densities (<4 individuals/ha; O’Farrell & Uptain, 1989; Price &
Endo, 1989) in small patches of transitional habitat or along roadsides (Brock & Kelt, 2004), providing some support for the notion that it could benefit from habitat corridors to improve population connectivity. Moreover, modeling of metapopulation dynamics in other kangaroo rats indicated that immigration that contributed to local population growth was greater from nearby populations than from populations at a distance (Sanderlin, Waser, Hines, & Nichols, 2012).

Here we evaluate the efficacy of translocation as a recovery strategy to establish new populations for at-risk species. Specifically, we use SKR to evaluate translocation success by: (1) estimating the population density of the post-release population over a span of 9 years; (2) measuring genetic diversity and population structure of the release population and extent of admixture of our founder groups from different source sites; and (3) assessing parentage of litters produced at the release site to determine if released founders contributed to the long-term success of the new population through reproduction.

2 METHODS

2.1 Translocation, post-release monitoring, precipitation, population estimation and genetic sample collection

2.1.1 Translocation

We studied SKR on and adjacent to the Southwestern Riverside County Multispecies Reserve “Reserve” in southern California (33° N, 117° W, mean elevation 472 m) from 2008 to 2017. Detailed translocation methodology was described by Shier and Swaisgood (2012). In summary, in 2008 we selected a release site (“Plateau”, 33°34’53.82” N, 117°01’33.12” W) that was located within the historical range of the SKR, and contained appropriate soils (deep well drained with a loamy texture), slope and vegetation type (non-native open grass dominated; USFWS, 1997). We conducted sign surveys and trapping which revealed no resident SKRs and prepared the site for translocation by mowing to reduce ground cover and installing acclimation cages (Shier & Swaisgood, 2012). We captured 54 SKRs (39 adults and 15 juveniles) from two source sites, Metropolitan Water District land (n = 23, “MWD,” 33°34’22.19” N, 117°04’06.96” W), and private land (n = 31, “El Sol,” 33°33’30.09” N, 117°02’16.26” W) adjacent to the Reserve, affixed radio transmitters to all individuals, and translocated them into acclimation cages at the Plateau (Figure 1). Founders from source sites were translocated in the same locations at the release site either in intact neighbor groups or in groups composed of unfamiliar individuals.

In 2009, we followed the same methodology except that we increased suitable habitat on the eastern portion of the Plateau using a prescribed burn rather than mowing to reduce nonnative ground cover. The 2009 release area was adjacent and connected to the 2008 release site and unoccupied as verified by pre-translocation sight surveys. Founders for the 2009 translocation were captured from a source site in and around the Lake Skinner campground (“Parking Lot,” 33°35’20.95” N, 117°02’05.74” W; N = 45; 30 adults and 15 juveniles), and translocated the newly improved release area. The source and release sites were from 1.49 to 3.93 km apart (Figure 1), well beyond the maximum dispersal distance documented for this species (1.04 km; Price et al., 1994) and trapping data indicated that no other SKR populations existed between the source and release sites (Shier, unpublished data). Upon capture, we individually marked each animal with numbered ear tags (National Band and Tag, Newport,
Kentucky), and took data on age, sex, reproductive condition, and weight.

2.2 | Post-release monitoring

Following the 2008 release, we trapped the receiver site 5 nights each month (months 1 to 12 post-release), ear tagged all unmarked SKR and used the number of newly emergent offspring to assess litter size (Shier & Swaisgood, 2012). Because we fit each SKR founder with a radio-transmitter, we were able to verify that our 5 nights of trapping was sufficient to capture all founders that remained at the release site in the first 3 months following release. Relative to larger rodents (Weigl, 2005), kangaroo rats have a short life span (24–50 months; Jones, 1993), and following the 2008 translocation that included mostly adult animals we documented a decrease in survival of translocated animals beyond 6 months, and a concomitant increase in reproductive success as measured by offspring emergence from burrows established by translocated SKRs. Thus, we reduced the frequency of our monitoring following the 2009 release to 5 nights of trapping at 1, 3, 6, and 12 months.

We continued to assess numbers of SKRs at release sites over an additional 7 years following release (2010, 2011, 2012, 2013, and 2017) in order to assess long-term population persistence. However, because the Plateau release site extended over 8 ha of habitat managed for the SKR, from 2010 to 2017, and sign surveys indicated that the entire site was occupied; we estimated SKR densities rather than attempting to trap the entire site. To do this, we set up 38, 30 m grids with 10 m trap spacing (4 × 4 trap grids). We randomly chose approximately one-half (18 of the 38) grids each year and trapped SKRs for 4 or 5 consecutive nights, once each year between July and November for a total of 13,824 trap nights. We trapped during new moon to maximize capture probability.

2.2.1 | Precipitation

We utilized data from the Global Historical Climatology Network (Menne et al., 2012; Menne, Durre, Vose, Gleason, & Houston, 2012) and Palmer Index (NOAA 2020) and calculated monthly precipitation for the region averaged over 75 years (1943–2017). We then compared monthly precipitation for November through February, during all years of the study (2008–2017) to calculated monthly averages. Winter rains during this period have been shown to drive vegetation growth and contribute to Heteromyid reproduction (Kenagy & Bartholomew, 1985).

2.3 | Genetic sample collection

For each captured SKR, we collected a tiny sliver of tissue from the edge of the ear for genetic analysis. Ear snips are a common method for collection of genetic data in the family Heteromyidae (Alexander & Riddle, 2005; Loew, Williams, Ralls, Pilgrim, & Fleischer, 2005; Metcalf, Nunney, & Hyman, 2001; Waser, Busch, McCormick, & DeWoody, 2006), have been used with the SKR (Metcalf et al., 2001) and provide ample genetic data for analysis of parentage, genetic relationships and dispersal (Waser et al., 2006). Tissue samples were stored in 100% ethanol at −20°C until DNA extraction.

2.4 | DNA extraction, microsatellite development, and polymerase chain reaction

We collected and used 301 genetic samples in this study, including 30 El Sol founders, 21 MWD founders, 64 Parking Lot founders, and 186 post-release individuals at the Plateau release site sampled over a span of 5 years post-release. We extracted DNA via a column-based method using the QIAamp DNA Mini Kit (Qiagen Inc.) following the manufacturer’s protocol, and then stored it at −20°C.

We contracted the Savannah River Ecology Laboratory at the University of Georgia to develop the microsatellite library using 454 sequencing technology. Microsatellite loci were initially screened from a pool of 150 loci that seemed suitable according to algorithms implemented in the programs MSATCOMMANDER and PRIMER 3—that is, desirable microsatellite repeat motif (tetra-nucleotide), no primer dimer, reasonable polymerase chain reaction (PCR) conditions, etc. In order to reduce costs, for each of these candidate loci, we designed one primer with a 20-base “long tag” (’5-CGAGTTTCCCAAGTACGAC-3’) to allow for dye-labeling of PCR products during amplification using a third, 6-FAM-labeled primer with a corresponding sequence tag (i.e., “three-primer” PCR of [Schuelke, 2000]). We also included a “short tag” on the opposite primer (GTCT) to promote adenylation, thereby reducing ambiguities in genotyping due to multiple peaks (Brownstein, Carpten, & Smith, 1996). Evaluation of these markers resulted in the final set of 25 species-specific polymorphic loci used in this study (GenBank accession numbers KX214306-KX214330). Fluorescently labeled primers were obtained, replacing the formerly “long tagged” primer, allowing us to do multiplex PCR (Table S1).

We performed PCR reactions in a final volume of 12.5 μL containing 6.25 μL 2× Qiagen Multiplex PCR Master Mix, 1.25 μL 5× Q-solution, 0.25 μL primer mix...
We evaluated microsatellite markers at the population level: MWD; El Sol; Parking Lot; and Plateau 2009, 2010, 2011, 2012, and 2013. Exact tests to detect deviations from Hardy–Weinberg equilibrium and a genotypic equilibrium test for linkage disequilibrium were calculated using default settings in GENEPOP 4.1 (Raymond & Rousset, 1995; Rousset, 2008). Results from exact tests indicated one locus deviated statistically from Hardy–Weinberg equilibrium (Dst 1318) across all populations. Consequently, we discarded this locus.

The software GenAlEx (Peakall & Smouse, 2012) was used to calculate the probability of identity (PiSD) and probability of identity for full siblings (PiSibs) (Waits, Chapuis & Estoup, 2007). FREENA corrects CHECKER (van Oosterhout et al., 2004) and FREENA alleles and genotyping errors using the software MICRO-CHECKER also found no evidence for genotyping error due to large allelic dropout and stuttering. There were 48–52 replicate genotypes in which genotyping error rate was hand-calculated for each locus. The highest genotyping error rate observed was 0.02 at loci Dst3666 and 3066.

2.5 | Microsatellite variation

We evaluated microsatellite markers at the population level: MWD; El Sol; Parking Lot; and Plateau 2009, 2010, 2011, 2012, and 2013. Exact tests to detect deviations from Hardy–Weinberg equilibrium and a genotypic equilibrium test for linkage disequilibrium were calculated using default settings in GENEPOP 4.1 (Raymond & Rousset, 1995; Rousset, 2008). Results from exact tests indicated one locus deviated statistically from Hardy–Weinberg equilibrium (Dst 1318) across all populations. Consequently, we discarded this locus.

The software GenAlEx (Peakall & Smouse, 2012) was used to calculate the probability of identity (PiSD) and probability of identity for full siblings (PiSibs) (Waits, Luikart, & Taberlet, 2001) using the remaining 24 loci. Resulting calculations showed the strong exclusionary power of the loci to identify unique individuals with a PiSD of 1.3 \times 10^{-29} and PiSibs of 5.9 \times 10^{-11}, thus we concluded that these 24 loci were suitable for population genetic analyses. Results from linkage disequilibrium tests indicated no pairs of loci with significant deviations across all populations; therefore, the remaining loci were included for further analysis.

We further assessed markers for evidence of null alleles and genotyping errors using the software MICRO-CHECKER (van Oosterhout et al., 2004) and FREENA (Chapuis & Estoup, 2007). FREENA corrects FST values for null alleles using the INA method and computes 95% confidence intervals based on bootstrapping over all loci (10,000 bootstrap replicates). Significance at an initial p-value of .05 was corrected for multiple comparisons using the B-Y False Discovery Rate method (Benjamini & Yekutieli, 2001). There was some evidence for null alleles; however, uncorrected pairwise FST values fell within the 95% confidence interval for FST values corrected for the presence of null alleles, indicating that null alleles did not have a significant effect on the genetic differentiation estimates. Therefore, we retained all data for further analyses. MICRO-CHECKER also found no evidence for genotyping error due to large allelic dropout and stuttering. There were 48–52 replicate genotypes in which genotyping error rate was hand-calculated for each locus. The highest genotyping error rate observed was 0.02 at loci Dst3666 and 3066.

2.6 | Data analysis

2.6.1 | Post-release monitoring

We were interested in long-term translocation success as opposed to individual fates; therefore, we used the post-release trapping data from 2010–13 and 2017 to estimate population densities using spatial capture-recapture (SCR) models for closed-populations (Efford, Dawson, & Borchers, 2009; Royle et al., 2013; Royle & Young, 2008). Because the trapping data for each year were collected over 5 consecutive nights, the likelihood of significant recruitment or loss was negligible and we can assume population closure within each year (Otis, Burnham, White, & Anderson, 1978a). SCR models use individual capture histories to determine the parameters g0 (the capture probability of a trap being in the center of the home range), and \( \sigma \) (the spatial scale over which the capture probability declines). We used multi-session models that treat data from each year as a session, allowing us to share parameters across years. We used a half-normal detection function and a buffer of 200 m around the traps to define the state-space. We also applied a habitat mask that omitted areas of the plateau with habitat unsuitable for SKR occupation. We tested a variety of candidate models (g0 and \( \sigma \) constant or varying by session, and a behavioral response model where detection probability changes after the first capture) and selected the best model based on the Akaike information criterion corrected for smaller sample sizes (AICc; Burnham & Anderson, 2002). Models were analyzed in a maximum-likelihood framework in the package secr 4.2.0 (Efford, 2020) in R (R Development Core Team, 2019).

2.6.2 | Microsatellite variation

We calculated genetic diversity of each population as described by observed (H0) and expected heterozygosities (H0) using GENALEX 6.5 (Peakall & Smouse, 2012). Inbreeding coefficients (FIS) per population were estimated using FSTAT 2.9.3 (Goudet, 2001), and HP-RARE (Kalinowski, 2005) was used to obtain allelic richness (AR) and private allelic richness (PA) averaged over all loci by rarefaction, incorporating sample size variation. We calculated AR for all populations and PA using only founder populations. We calculated effective population size (Ne) estimates for post-translocation years 2010 to
2013 based on the linkage disequilibrium (LD) method implemented in LDNE1.31 (Waples & Do, 2008) selecting 0.02 as the lowest allele frequency used and obtaining 95% confidence intervals through jack knifing. N_e/N ratios were calculated using population density estimates from field trapping data as described above.

2.6.3 Population structure

We calculated genetic differentiation using GENODIVE version 2.0b27. We used Wright’s pairwise F<sub>ST</sub> to quantify variance in allele frequencies among populations (Weir & Cockerham, 1984) and Jost’s D (Jost, 2008) as a supplementary measure of genetic differentiation as it performs better when markers are highly variable (Meirmans & Hedrick, 2011). We assessed statistical significance for F<sub>ST</sub> values via exact tests (Meirmans & Van Tienderen, 2004). Significance was based on initial p-value of 0.05 and was corrected using the B-Y method (Benjamini & Yekutieli, 2001). We assessed population structure among the founder populations and evidence for admixture at the release site using a non-spatial Bayesian clustering analysis implemented in STRUCTURE 2.3.2 (Pritchard, Stephens, & Donnelly, 2000) with all source and post-translocation samples pooled into a single dataset (n = 301). We implemented the analysis with typical default settings, including an admixture model with correlated allele frequencies. We tested each population number (K) ranging from 1 to 10. For each value of K, we ran 10 independent replicates with a burn-in period of 100,000 steps followed by 1,500,000 iterations. The most likely true value of K was inferred using methods described by Evanno, Regnaut, & Goudet, 2005. We then used STRUCTURE to determine proportional membership (q-value) of each individual to each of the inferred genetic clusters. In general, STRUCTURE rarely assigns an individual to a single population with a q-value of 1.0 (Bohling et al., 2013), and this was observed here as well. Therefore, we use a q-value of 0.9 or greater as conservative evidence of an individual assigning to a single genetic cluster with no admixture. Offspring were assigned parents from different sites; if that offspring’s proportional membership coefficient was split approximately evenly among the two genetic clusters corresponding to the origin of the inferred parents (i.e., q-value > 0.3 for each cluster).

Population differentiation was also assessed using a multivariate approach. The Discriminant Analysis of Principal Components (DAPC) feature in the R package, ADEGENET, was used to determine the possible number of genetic clusters (Jombart et al., 2010) using a retention of 60 PC axes and three discriminant functions. The number of clusters (K) were varied from 1 to 10. The optimum K value was chosen based on the lowest value of K that reflected the least changes in BIC (Jombart et al., 2008).

2.6.4 Parentage analysis

We used CERVUS 3.0.3 (Kalinowski, Taper, & Marshall, 2007) to infer parentage using a strict exclusion analysis without sex information. Genotypes were simulated for each post-translocation year (2009–2013) using candidate parents that represented the pool of founders and any post-translocation individuals from the previous years. Simulations were performed with 10,000 offspring and a 1% error rate (i.e., 0.01 proportion of mistyped loci). Due to the changing proportion and pool of candidate parents genotyped each year following translocation, input values for the simulated number of candidate parents and the proportion of candidate parents sampled were modified for each analysis. The simulated number of candidate parents was chosen to reflect the empirical pool of candidate parents for that post-translocation year and we decreased the proportion of candidate parents sampled from 0.90, 0.70, 0.40, 0.30, to 0.2 (2009–2013) to reflect the reduced sampling in relation to the entire population each year post-translocation.

By assigning offspring born at the release site to translocated parents, population growth at the release site is directly attributable to the reproductive success of translocated individuals. Alternatively, the presence of offspring at the Plateau release site that could not be assigned to the translocated SKR could indicate recruitment of immigrants into the translocation site or reproduction between unsampled SKR that are descendants of the founders.

The average non-exclusion probability for a single parent-offspring relationship was 3.77 x 10⁻⁷ (1.64 x 10⁻⁷ to 5.14 x 10⁻⁷) across the five post-translocation years, which corresponds to the probability that an incorrect parent-offspring relationship will be assigned. The average non-exclusion probability for a parent pair was 3.86 x 10⁻¹⁸ (1.49 x 10⁻¹⁷ to 9.70 x 10⁻²⁰). We permitted no more than one mismatch for parent-offspring relationship to be highly conservative (parentage assignments that involved accepted mismatches are noted with an asterisk in Table S3). Possible explanations for these close but non-perfect matches could be mutation, null alleles, or genotyping error.

2.6.5 Genetics and fitness

We used a Poisson regression in STATA14 (StataCorp, 2015) to examine potential effects of outbreeding on fitness by
The age structure and density estimates of SKR at the Plateau following translocations in 2008 and 2009. Population growth is illustrated by the proportion of juveniles in the trapped population (Table 1).

| Year | N  | Adult | Juvenile | Proportion of juveniles | Density (SE)/ha | 95% confidence interval for density |
|------|----|-------|----------|-------------------------|----------------|-----------------------------------|
| 2010 | 176| 140   | 36       | 20.50%                  | 44.1 (4.5)     | 36.1–53.8                         |
| 2011 | 159| 112   | 47       | 29.60%                  | 44.3 (4.3)     | 36.7–53.5                         |
| 2012 | 105| 93    | 7        | 7.00%                   | 24.0 (2.7)     | 19.3–30.0                         |
| 2013 | 49 | 49    | 0        | 0.00%                   | 10.9 (1.7)     | 7.9–14.8                          |
| 2017 | 153| 119   | 21       | 15.00%                  | 52.0 (5.6)     | 42.1–64.1                         |

3.2 | Microsatellite variation

The highest levels of allelic richness and private alleles were observed in the Parking Lot population followed by El Sol and MWD (see summary statistics Table 2). Genetic diversity estimates from the Plateau are comparable to that observed at the Parking Lot population (AR = 7.22; Ho = 0.762), and continued to retain high levels of genetic diversity throughout 2013 with an average allelic richness of 7.61 (7.14–7.93) and average observed heterozygosity of 0.745 (0.725–0.758). There were no signs of inbreeding in any population as indicated by the negligible inbreeding coefficients (F_IIS = 0.129–0.039). N_e/N ratios at the Plateau steadily increased from its first year and peaks in 2012 at N_e/N of 0.77–1.40 followed by a decrease the following year to 0.39–0.51.

3.3 | Population structure

In population genetics, differentiation based on Fst levels can be categorized as little (<0.05), moderate (0.05–0.15), great (0.15–0.25), or very great (>0.25) (Balloux & Lugon-Moulin, 2002; Hartl & Clark, 1997). Our results indicated moderate to great levels of genetic differentiation among the three source sites despite their relatively close geographic proximity (Jost’s D = 0.33–0.44; F_ST = 0.102–0.170; Figure 1). Among the founder populations, MWD was the most highly differentiated from the other two populations (Table 3). Observed levels of Fst among founder populations were higher than those of some kangaroo rat species for which interpopulation distances were greater (D. inges; Loew et al., 2005; D. elator; Pfau, Goetz, Martin, Matocha, & Nelson, 2019). Post-translocation Plateau populations from 2009 to 2013 showed low genetic differentiation from each other as expected (F_ST = 0.004–0.032; Jost’s D = 0.001–0.01), as well as to the source populations (F_ST = 0.134–0.248; Jost’s D = 0.038–0.094).

STRUCTURE analysis produced strong evidence for population structure. The highest value of ΔK was...
achieved at $K = 3$ (Table S4). Individual proportional memberships under a model of $K = 3$ populations show a pattern of genetic partitioning largely consistent with the geographic origin of the source samples (Figure 2). Thus, our findings affirmed Price’s earlier results that showed limited dispersal in SKR (Price et al., 1994). Despite being located within only a few kilometers of one another, it appears that the allelic variation present at the 24 microsatellite loci surveyed is sufficient for genetic discrimination of these founder populations. Because observed pairwise $F_{ST}$ values are in the range required to confidently identify individuals with multi-population ancestry when using 24 loci, based on simulation (Vaha & Primmer, 2006), we are highly confident that observed admixture is robustly estimated. Results from the population structure analysis using DAPC inferred 5 clusters based on the lowest BIC value observed. However, it was evident from the scatterplot (Figure S2a) and membership of assigned populations to inferred clusters that overclustering by the software classified admixed individuals as unique clusters, therefore, $K = 3$ is most likely number of genetic clusters.

The Bayesian clustering analysis suggested that, in the year after the initial translocations (2009), F1 individuals with signs of admixture between El Sol and MWD were produced at the Plateau release site (Figure 2). In year 2 (2010) at the Plateau, the analysis also identified several individuals with admixture between the two clusters identified in 2009 and the Parking Lot site, which was translocated to the Plateau in 2009. Thus, these results are consistent with the translocation strategy carried out over the course of those 2 years at the Plateau.

In 2009 at the Plateau, the mean proportional membership of each individual to the El Sol cluster was 0.52 and that of MWD was 0.42. By 2010, 1 year after the release site was supplemented with founders from the Parking Lot source site the following year, the genetic contribution from each source population converged towards equilibrium (with equal representation of the founder populations) each successive year between 2010 and 2013 (Figure 3). Individuals with $q$-values greater than 0.90 (i.e., over 90% proportional membership to a single source population) were compared among the source sites and the Plateau over a period of 5 years
post-translocation from 2009 to 2013. As expected, source populations had significantly more individuals with \( q \)-values greater than 0.9, with MWD having the highest number of individuals in the population (95.2%) followed by El Sol (86.7%) and Parking Lot (82.8%). In contrast, only 57.1% of the Plateau population had \( q \)-values greater than 0.90 in the first year, and those numbers declined in subsequent years from 57.1% to 24.2%, 21.2%, 3.0%, and 6.3%.

### 3.4 Parentage analysis

We were able to assign at least one parent to 40 of the individuals sampled at the Plateau release site in 2009 (Table S3). In seven of the eight cases in which an individual was assigned parents from different sites, that offspring’s proportional membership coefficient was split approximately evenly among the two genetic clusters corresponding to the origin of the inferred parents (i.e., \( q \)-value > 0.3 for each cluster). In general, the results of the parentage analysis largely corroborate the results of the population structure analysis. Cases in which neither parent could be inferred were most likely a result of incomplete sampling. Field surveys and demographic modeling have shown that if conditions are favorable (i.e., years with higher the average rainfall) SKR can produce multiple litters in a single year, and first year females can reproduce in the year that they are born (2–5 litters/year; O’Farrell & Clark, 1987; Price & Kelly, 1994; USFWS, 1997), and thus annual sampling may not have been sufficient to identify all offspring produced at the release site. An alternative explanation is that SKR from surrounding areas immigrated to the release site post-translocation and produced the offspring for which we were unable to infer parentage. However, this explanation is not supported by the data, as we would expect any resident the population structure analysis did not identify a cluster genetically distinct from the founder populations.

With every successive year, fewer parents were assigned to offspring due to the increasing pool of unsampled candidate parents in relation to the entire population. Nonetheless, at least 18% of the offspring each year could be assigned to at least one sampled parent. There is evidence of successful breeding of F1 to F4 individuals (assuming one breeding a year) for SKR that were newly sampled as juveniles at the release site.
We demonstrated the ability to utilize DNA microsatellite markers to assess translocation success from a genetic standpoint at a very fine-scale, where previous studies have been limited to few markers and relied on basic genetic similarity as a proxy for translocation success (Germano, Saslaw, Smith, & Cypher, 2013). Our genetic data provide a second line of evidence that translocation of the SKR was highly successful, and that the population of the SKR established at the release site was the result of the translocation rather than recruitment in response to habitat improvement.

Using parentage exclusion, we found numerous instances of assignment, across all translocation efforts, of one or both parents of juvenile SKR collected on the translocation sites. This is noteworthy given the extremely low probability of assignment being observed due to chance alone ($3.71 \times 10^{-7}$ and $3.68 \times 10^{-18}$ for a single parent or parent pair, respectively). Because the identified parents had been translocated, this provides unambiguous evidence for reproductive success of translocated SKR. While there are many compelling examples of parentage, this pattern was most striking following the 2008 translocation of SKRs from the MWD and El Sol sites to the Plateau release site, likely because sampling of the translocated individuals in 2008 was the most comprehensive—that is, genotype data were available from almost all of the translocated individuals. This allowed for a direct assessment of the reproductive success of the individuals translocated from MWD and El Sol in 2008 revealing many interesting groupings, including juveniles produced by parents from the same and different source populations. We were able to assign at least one specific parent to 40 of the animals—providing strong evidence that translocated individuals have successfully reproduced in their new environment.

In general, the results of the parentage analysis largely corroborate the results of the population structure analysis. Cases in which neither parent could be inferred were most likely a result of unsampled descendants of founders. Field surveys and demographic modeling have shown that if conditions are favorable (i.e., years with higher the average rainfall) SKR can produce multiple litters in a single year, first year females can reproduce in the year that they are born (2–5 litters/year; O’Farrell & Clark, 1987; Price & Kelly, 1994; USFWS, 1997), and thus, annual sampling may not have been sufficient to identify all offspring produced at the release site. Aside from the three founder populations, structure analyses did not identify additional unique clusters that would indicate recruitment of immigrants into the translocation site. It is possible that an undetected low-density resident population present off of the release site but within dispersal distance with similar genetic signatures, as the
founder populations would remain undetected in our structure analyses. However, this is unlikely as we would expect any resident populations to be genetically distinct based on the levels of differentiation observed in the three founder populations despite close proximity.

Although every successive year post-translocation resulted in fewer individuals for which we were able to assign both parents, we were able to assign parentage for at least 18% of the offspring sampled at the release site. Assigned parents include individuals from one of the source sites or F1-F4 individuals from the release site, which provides evidence of successful reproduction across multiple generations and is an important benchmark for fitness. For example, an individual sampled in 2010 assigned to be the offspring of two F1 parents: one F1 from an El Sol and MWD parent; the other F1 had both MWD parents (one identified by genotype to a sampled founder, the other assigned to the MWD population by Bayesian clustering analysis). We were also able to identify examples of reproductive success of individuals up to 4 years post-translocation. For example, an F1 individual at the Plateau site reproduced the following year (2009) and again 3 years later in 2012. Four other individuals reproduced in 2 separate years.

Past studies of SKR have suggested limited dispersal in the species (Price et al., 1994), encouraging the use of multilocus genotyping to infer interbreeding of translocated individuals derived from different source populations. This was indeed the case with the source populations showing surprisingly strong genetic differentiation over short distances. The ancestry plot (Figure 2) reveals a strong association between geography and population genetic structuring, with 86% of source individuals having the largest proportion of their allelic diversity (q-value > 0.9) assigning to the site from which they were sampled.

While other studies seeking to use STRUCTURE to detect translocated individuals have had little success due to limited geographically-associated differentiation or a pattern of isolation-by-distance (Frantz et al., 2006; Raisin et al., 2012), the application of population clustering analyses in this study identified significant population subdivision and also provided evidence for interbreeding of individuals from the source populations of the translocated individuals.

Our results also suggest that despite mixing populations that displayed clear genetic differentiation, there was no evidence of outbreeding depression. Litter size of founder females that mated with males from their same source population did not differ from those founder females that mated with males from a different source population. Further, litter size of F2 pups was the same as the litter size of F1 pups produced by founder females. These results suggest that despite mixing source populations with moderate to great levels of genetic differentiation, outbreeding depression was not apparent, providing support for the growing body of literature that suggests that outbreeding depression may not be as much of a concern as inbreeding depression in the management of small populations (Frankham et al., 2011; Whiteley, Fitzpatrick, Funk, & Tallmon, 2015).

Finally, our results provide genetic evidence for the benefit of selecting release sites to establish connectivity with existing populations. While landscape connectivity may hamper early establishment (Parlato & Armstrong, 2013), if released populations are to persist, multiple subpopulations are required to maintain exchange and minimize the risk of local extinction (Kramer, Revilla, Wiegand, & Breitenmoser, 2004; La Morgia, Malenotti, Badino, & Bona, 2011; Price & Gilpin, 1996). As fragmentation limits natural processes of migration and dispersal, protected populations in reserves will be subject to differentiation due to drift and inbreeding. The relatively high population differentiation observed among the SKR source sites supports a strong role for genetic drift in these populations and underscores the significance of genetic monitoring and population management for genetic maintenance and recovery.

Despite the historical failure of heteromyid translocation efforts, our long-term study illustrates how the development of species-specific best practices led to an effective strategy for SKR recovery. More broadly, efforts that use a systematic hypothesis-testing framework, genetic evaluation and long-term monitoring offer great promise in improving translocation outcomes for at-risk species.

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CONFLICT OF INTEREST

The authors declare no conflicts of interest exist.

AUTHOR CONTRIBUTIONS

Debra M. Shier conducted the translocation and post-release surveys, collected all genetic samples and analyzed ecological data. Asako Y. Navarro, Steven M. Thomas, and Claire B. Mullaney conducted genetic analyses. Debra M. Shier, Steven M. Thomas, and Asako
Y. Navarro wrote the first draft of this manuscript. Oliver A. Ryder revised the manuscript. Shauna N. D. King and Mathias Tobler conducted population modeling and revised the manuscript.

**DATA AVAILABILITY STATEMENT**
Microsatellite primer sequences have been uploaded to GenBank (https://www.ncbi.nlm.nih.gov/nuccore; accession numbers KX214306–KX214330). Population estimation data are available from Mendeley data (Shier, 2021).

**ETHICS STATEMENT**
This research followed guidelines by the American Society of Mammalogists (Sikes & Anim Care Use Comm Amer Soc, 2016) and was approved under San Diego Zoo Wildlife Alliance animal care and use protocols (09-007, 13-007, 15-002).

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

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