



Policy analysis

Saving all the pieces: An inadequate conservation strategy for an endangered amphibian in an urbanizing area

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ABSTRACT

Species conservation often focuses on preserving populations on remnant habitat patches, typically without evidence that this approach is sufficient for halting declines. We employed a 19-year dataset to examine the adequacy of this approach for recovering the Sonoma County distinct population segment of California tiger salamanders (SCTS; *Ambystoma californiense*), California, USA, which now exists almost entirely in remnant habitat patches designated as preserves across a rapidly urbanizing landscape. We estimated relative SCTS larval densities from standardized annual surveys from 2002 to 2020 across 118 vernal pools in eight preserves. We found that relative larval SCTS densities decreased by 48% over the study period, indicating that current efforts to conserve SCTS are inadequate for long-term viability. Increased densities were only observed at the single study preserve where SCTS were introduced. Temporal trends in larval density among preserves were best explained by the number of pools available to SCTS, and the ability of breeding pools to retain water throughout the larval period. Specifically, preserves with >1 breeding pool and ≥1 breeding pool that held water for at least two months following the breeding season (into late April) even in dry years had substantially lower rates of larval decline. Active conservation management of preserves, including provision of multiple breeding pools, at least some of which are resilient to variable future precipitation regimes, will be required to effectively conserve SCTS. We expect these findings to apply broadly to the conservation of many species of pool-breeding amphibians.

1. Introduction

Efforts to conserve imperiled and declining species often emphasize preserving habitat remnants where the species still persists (Possingham et al., 2015). Success of this approach requires protection of enough habitat to support populations and metapopulations that can withstand the stochasticity inherent in genetic, demographic, and environmental processes (Soule and Simberloff, 1986; Lande, 1993; Hanski, 1998). Variation in habitat quality and specialized requirements of the species of concern, including in some cases the need for more than one habitat type (e.g., Baldwin et al., 2006; Jackson et al., 2019), complicate the requirements for conservation success. Additional challenges are expected in the future with continuing degradation of the matrix in which protected habitat patches are located (Watling et al., 2011), climate

change, and the interactions between climate change, habitat loss, and habitat fragmentation (Mantyka-Pringle et al., 2012; Segan et al., 2016).

Given these challenges, the effectiveness of conserving species through the preservation of habitat remnants with relict populations cannot be assumed. Ongoing assessment of conservation performance, including population trends of taxa of concern, is essential (Gerber et al., 1999; Martin et al., 2007; Thapa et al., 2017). Such assessments should be designed to gauge the success of this strategy before viable alternatives are no longer available or populations have declined to unrecoverable levels (e.g., extinction debt; VanderWerf et al., 2006; Kuussaari et al., 2009; Semlitsch et al., 2017). Furthermore, information produced through ongoing assessment is useful for prioritizing species for conservation efforts (Bernardo et al., 2019) and identifying promising actions for species recovery (Thapa et al., 2017).

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Amphibians are the most threatened class of vertebrates (Stuart et al., 2004; González-del-Pliego et al., 2019), and present a particularly complex conservation challenge. Habitat loss and fragmentation is the greatest threat to the group (Cushman, 2006), and many species require both aquatic and terrestrial habitat (Wilbur, 1980), as well as movement corridors between those habitats (Pittman et al., 2014). In areas of intense landscape conversion (e.g., urbanizing areas) that are experiencing outright loss of aquatic and terrestrial habitat (e.g., Houlihan and Findlay, 2003; Rubbo and Kiesecker, 2005), amphibians may be reduced to small, isolated habitat patches in a matrix of unsuitable land cover (Semlitsch and Bodie, 1998). This scenario leads to genetic (Titus et al., 2014) and demographic (Pickett et al., 2014) hazards for small populations, impaired metapopulation function (Heard et al., 2012), and reduced habitat quality (Riley et al., 2005; Rubbo and Kiesecker, 2005). Further, amphibians' ectothermic physiology (Rohr and Palmer, 2013), limited vagility (Hillman et al., 2014), and susceptibility to negative effects of anthropogenic land uses (Cayuela et al., 2015) and migration barriers (e.g., roads; Gibbs and Shriver, 2005) are likely to severely constrain their resilience in response to future climate change (Struecker and Milanovich, 2017).

The California tiger salamander (CTS; *Ambystoma californiense*; Shaffer et al., 2004) is a federally protected vernal pool-breeding species endemic to grasslands in California, USA. Habitat loss is the leading threat to CTS (Fisher and Shaffer, 1996; Davidson et al., 2002) across all three federally designated distinct population segments (DPSs) of the species (i.e., geographically and/or genetically separate populations of the species with unique conservation needs). The Sonoma California tiger salamander DPS (SCTS) was listed as Endangered under the US Endangered Species Act in 2003 (USFWS, 2003). SCTS occur in vernal pools and adjacent terrestrial habitats in a small portion of the Santa Rosa Plain and nearby lowlands, a rapidly urbanizing area north of San Francisco. Both the aquatic and terrestrial habitats of SCTS have been greatly reduced through widespread conversion of formerly low-intensity agricultural and undeveloped grasslands to urban, suburban, and intensive agricultural (e.g., vineyard) land uses (USFWS, 2016a). In 1994, it was estimated that the historic extent of vernal pool habitat on the Santa Rosa Plain had decreased by >85% (Patterson et al., 1994). Habitat loss has progressed since that time, with 7000–8000 ha of potential SCTS habitat remaining, most of which is highly fragmented (USFWS, 2016a).

To date, SCTS conservation efforts have focused primarily on the protection of existing breeding populations (herein “breeding population” refers to all SCTS that use a given pool for reproduction, assuming limited dispersal and switching between pools [Trenham et al., 2001]) on preserved remnant habitat patches (hereafter “preserves”) in the suburban/rural matrix (USFWS, 2005, 2016a). Because of continued expansion of human activities, SCTS habitat available for preservation is increasingly scarce and fragmented (Cook et al., 2006; USFWS, 2016a). As conservation options become foreclosed, it is important to know whether the current approach of conserving remnant SCTS populations is effective, whether it is likely to be effective in the future, and how it can be improved. A difficulty in answering these questions is the highly variable nature of amphibian population dynamics (Marsh, 2001), necessitating long-term studies to discern population trends. Further, though recruitment and survival of the terrestrial life stages are strong indicators of amphibian population dynamics (Biek et al., 2002; Vonesh and De la Cruz, 2002; Taylor et al., 2006), estimation of these vital rates is challenging due to the fossorial nature of post-metamorphic ambystomatid salamanders outside of the breeding season (Messerman et al., 2020). Consequently, the quantity and spatial and temporal extent of post-metamorphic data are necessarily limited.

One commonly employed alternative is to monitor larvae. Larval abundance and density are highly spatially and temporally variable (Greenberg et al., 2017), such that only long-term trends are likely to reveal population changes. Trends in larval density spanning generations may be the product of changes in adult breeding population size,

adult breeding effort, and/or aquatic survival rates, all of which are likely to have population-level effects.

Here, we use a 19-year record (2002–2020) of SCTS larval surveys at 118 pools across eight preserves on the Santa Rosa Plain to assess the effectiveness of current SCTS conservation efforts. We then identify habitat characteristics that are predictive of larval density to inform future SCTS preserve design and management efforts. Our eight study preserves comprise all of the known protected locations of SCTS breeding populations at the time of listing (USFWS, 2005). Seven of the eight preserves host remnant naturally occurring populations of SCTS; the eighth is a historically-unoccupied restored site where SCTS were introduced. Our results provide an outlook for SCTS in the face of current and expected threats, and indicate preserve-level management strategies that are likely to enhance the conservation of SCTS and ecologically similar pool-breeding amphibians.

2. Materials and methods

2.1. CTS breeding biology

CTS are adapted to a Mediterranean climate, where adults migrate to vernal pools from upland habitat to breed during rain events from November–February during the California wet season, which is typically the coolest period of the year and occurs November–March (Searcy and Shaffer, 2011). Females then deposit eggs within pools before returning to upland habitat. Aquatic larvae hatch 2–4 weeks after egg deposition. Following a minimum post-hatching development period of 10 weeks, surviving larvae metamorphose and move into the terrestrial habitat (Jennings and Hayes, 1994). As with all pool-breeding amphibians, pools must hold water throughout the embryonic and minimum larval development periods for the successful recruitment of metamorphs into the population (Pechmann et al., 1989). For many ambystomatids, it is also important that pools remain ephemeral to limit the establishment of fish and other predators (Maurer et al., 2014). We consider reproductive success to be the product of adult breeding and embryonic/larval survival to metamorphosis. Following breeding and metamorphosis, both juvenile and adult SCTS inhabit small mammal burrows throughout the dry season (Loredo et al., 1996; Trenham and Shaffer, 2005), and typically survive to 6 or 7 years of age (Trenham et al., 2000). The activities of CTS in their upland habitat are poorly understood, and the distance SCTS migrate from their breeding pools is unknown. Studies of CTS elsewhere indicate substantial movement, with 50% and 95% of CTS terrestrial populations estimated to occur within 504 m and 1703 m of the pool shoreline, respectively (Searcy and Shaffer, 2011; USFWS, 2016b). Federal designation of CTS habitat extends to 2092 m from a breeding pool's shoreline (USFWS, 2004).

2.2. Study area

Our study area consisted of eight preserves on the Santa Rosa Plain, Sonoma County, California, USA (38.45° N, 122.70° W; Fig. 1). These preserves are Alton (ALT), Broadmore North (BRN), Engel (ENG), FEMA (FEM), Hall (HAL), Scenic (SCE), Southwest Park (SWP), and Yuba (YUB). Study preserves range in area from 1.2 to 69.6 ha (Table 1). All preserves include upland habitat dominated by a mix of native and non-native grasses and forbs, and 1–55 vernal pools (Table 1). The study pools are shallow (typically <0.5 m deep) and feature sparse, low-stature vegetation or bare substrate. All pools are exclusively rain fed and typically dry in spring, with the longest-persisting pools holding water into June in drier years. Four preserves (ALT, ENG, HAL, and YUB) include human-constructed pools added as mitigation for the loss of natural wetlands and designed to mimic vernal pools (DFG, 2003). SCTS naturally occur at all preserves except ALT, which was stocked with SCTS larvae in 1996 (C. Patterson, personal communication) and adults in 2004 (W. Cox, personal communication). Connectivity between our study preserves is likely low due to the conversion of grasslands and low-

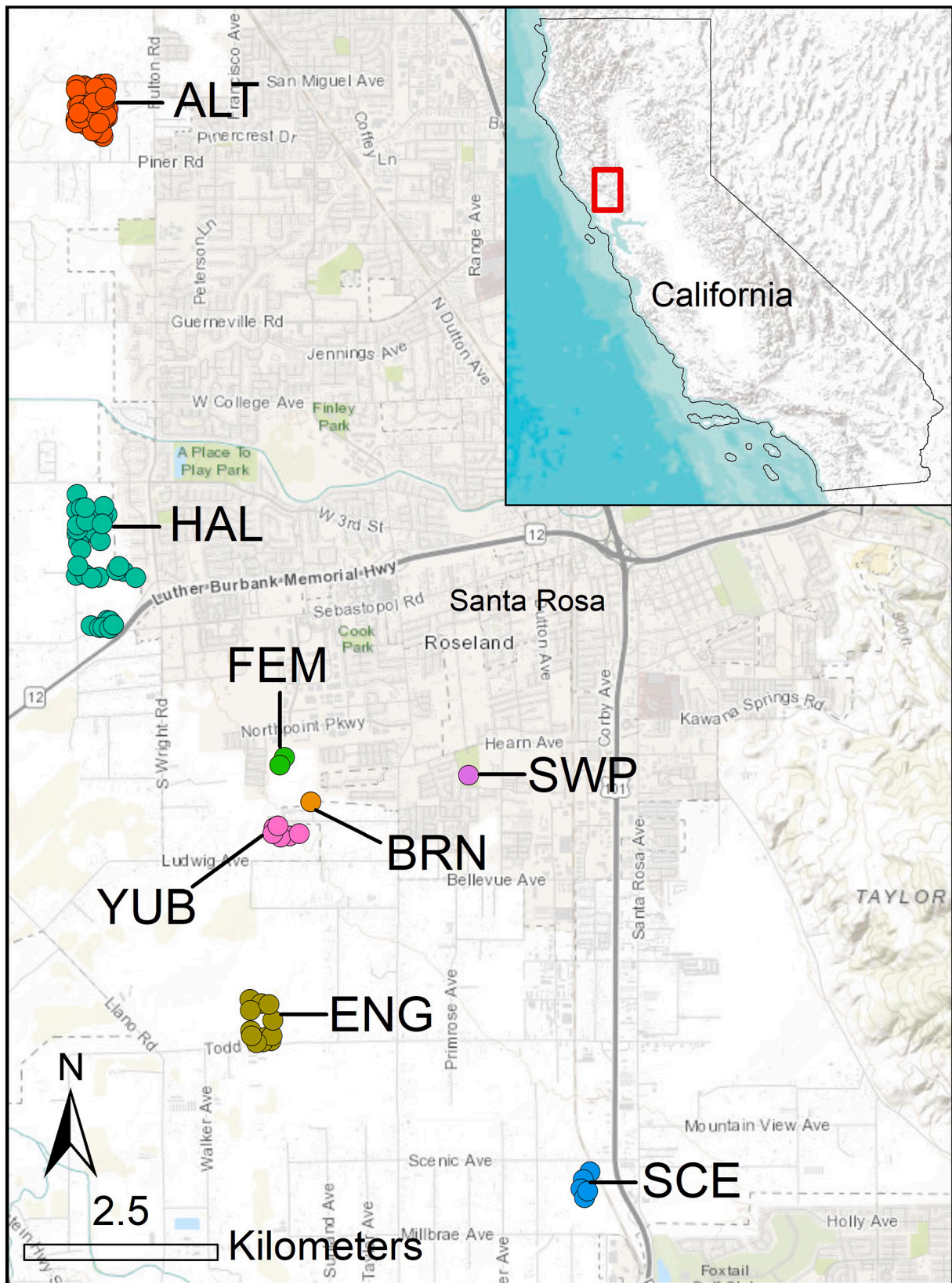


Fig. 1. Locations of the 118 study pools across eight preserves on the Santa Rosa Plain (see inset for location). All preserves host naturally occurring populations of SCTS except ALT, a restored site where SCTS were introduced.

Table 1

Study preserve characteristics across the study period (2002–2020). Standard deviations are presented in association with mean values.

	ALT	BRN	ENG	FEM	HAL	SCE	SWP	YUB
Mean larval density (larvae/min)	0.08 ± 0.30	0.65 ± 1.15	0.45 ± 1.10	0.22 ± 0.38	0.12 ± 0.38	0.40 ± 0.64	0.53 ± 1.33	0.20 ± 0.47
Predicted change in larval density (%)	+175 ^a	−100	−65 ^a	−50	−63 ^a	−42	−100 ^a	−30
Preserve area (ha)	18.2	5.3	16.2	32.0	69.6	9.3	1.2	4.9
Pools	55	1	12	2	35	5	1	7
Occupied pools ^b	17	1	10	2	17	4	1	4
Mean pool depth during surveys (cm)	11 ± 18	26 ± 7	20 ± 15	64 ± 28	23 ± 17	39 ± 21	57 ± 36	26 ± 15
Mean of max. pool depths (cm)	28 ± 14	40	34 ± 9	76 ± 30	33 ± 15	53 ± 19	114	41 ± 11
Mean of max. pool areas (ha)	0.86 ± 0.09	0.16	0.14 ± 0.12	1.53 ± 0.69	0.10 ± 0.10	0.05 ± 0.03	0.67	0.12 ± 0.10
Max. 2007 dry dates (Julian date)	166	95	104	166	138	118	95	118
Years surveyed	19	11	19	17	19	11	19	12
Suitable uplands (ha) ^c	1157	900	1644	832	1134	655	20	1063
Length of roads (m) within stated buffer distances from pools:								
High ^d								
504 m	867	0	0	0	2102	0	0	0
1703 m	3725	3290	1330	1333	8609	4247	2600	3393
2092 m	4676	4923	2751	4088	10,248	4473	3825	5115
≥Medium ^d								
504 m	867	0	0	0	2102	0	0	0
1703 m	3725	3290	1330	1333	8603	4700	3535	3393
2092 m	4676	4923	2751	4088	10,248	7544	5245	5115
≥Low ^d								
504 m	1678	0	1194	0	3311	1070	0	1100
1703 m	7309	6490	4911	3886	13,835	10,086	4621	6625
2092 m	9109	8523	7095	6971	18,534	14,199	6960	8795

^a The predicted preserve-specific change in larval densities over the study period significantly differs from zero.

^b Occupied in ≥1 survey year.

^c Representing the area of contiguous undeveloped land including preserve and area within 1850 m of the preserve without major isolating barriers (i.e., the area of habitat potentially accessible to SCTS at the preserve) as identified in 2015.

^d Low, Medium, and High represent traffic volume categories of 1000–5000, 5000–10,000, and >10,000 cars/day, respectively, within each buffer distance.

intensity agricultural lands to residential, commercial, and intensive agricultural land uses in recent decades (Patterson et al., 1994; USFWS, 2016a). As a result, we expect that SCTS breeding populations within each preserve function as isolated single populations or metapopulations (herein defined as breeding populations interconnected by dispersal events) of unknown viability (Trenham et al., 2001).

2.3. Larval surveys

To determine relative SCTS larval densities at study pools, we conducted standardized dipnet surveys as described in Heyer et al. (1994) in mid-March of each year from 2002 to 2020. We did not sample all pools and preserves in all years due to logistical limitations ($\bar{x} = 100.5 \pm 5.6$ SD pools sampled per year; Table 1). Surveys occurred after larvae had reached a detectable size and eggs were no longer seen in pools but before any larvae had metamorphosed, based on the timing of rain events and annual SCTS breeding activity (Cook et al., 2006). Wilson and Maret (2002) found a strong correlation between relative larval densities calculated from timed dipnet surveys and “true” larval densities estimated from thoroughly sampled box traps among three Eastern USA ambystomatid species. These authors also found that larval detection via dipnet sampling varied with habitat, with detection being lowest in the presence of woody debris and dense vegetation (Wilson and Maret, 2002). Because our study pools have little vegetative structure, we expect relative larval SCTS density from standardized timed dipnet surveys to be an even stronger predictor of true larval density in the present study system.

We took two approaches to reduce variation in detection probability throughout this study. First, we surveyed for larvae by sweeping standard “D”-shaped dipnets along the pool bottom and through the water column, sampling all aquatic habitat types in each pool (i.e., deep to shallow open water, and emergent and floating vegetation). Second, all surveyors (2–12 per survey) were trained in the field by the same person (D.G.C.) to ensure methodological consistency.

We timed surveys to allow calculation of capture rate per unit effort. Sampling duration varied with pool size (22.7 ± 31.7 person-minutes/pool; $n = 1933$ pool surveys). We identified all larval amphibians captured to species, recorded number of SCTS larvae, and released all

larvae at the point of capture after completion of the pool survey. We measured the maximum water depth of each pool immediately after sampling.

2.4. Environmental variables

To identify preserve characteristics that may influence SCTS larval densities across preserves, we collected additional information on each pool and the upland habitat surrounding each preserve. At the time of the 2007 survey, we visually located the transition between hydrophytic and upland-dominated vegetation around each pool as an indicator of long-term maximum pool fill boundaries, and used hand-held GPS units (GeoExplorer 3; Trimble, Sunnyvale, CA) to map these perimeters. We entered GPS data into a geographic information system (GIS) using ArcView software version 3.3 (ESRI, 2002), from which we calculated pool areas. In 2007, we also monitored study pools weekly after our larval survey to determine date of drying.

In 2015, we used Google Earth (Google LLC, Mountain View, CA) to determine the area of contiguous potential SCTS upland habitat around each study preserve. We defined potential upland habitat as undeveloped, rural residential, low-intensity agricultural, or preserve lands that were within 1850 m of the preserve (encompassing a larger estimated distance from the pool shoreline within which 95% of CTS are estimated to occur; Searcy et al., 2013), and not separated from the preserve by a barrier (e.g., major road or incompatible development).

Roads can pose a substantial hazard to migrating juvenile and adult SCTS (Bain et al., 2017). To determine whether the length and use of roads surrounding each preserve influenced changes in larval density, we accessed Sonoma County-maintained road length and traffic volume data collected from 2008 to 2020 (SCDTPW, 2020). Roads were categorized as having Low (1000–5000 cars/day), Medium (5000–10,000 cars/day), or High (>10,000 cars/day) traffic volumes. We then created buffers around each study pool of 504, 1703, and 2092 m—given the ecological relevance of these distances defined above (USFWS, 2016b)—using ArcGIS software version 10.7.1 (ESRI, 2019). We merged these buffers into a single shapefile for each preserve, and calculated the length of roads within each of the three aforementioned buffer distances with High, ≥Medium, and ≥Low traffic volumes.

Cumulative precipitation is a predictor of terrestrial ambystomatid surface activity—including foraging and the timing of breeding emigrations (Pechmann et al., 1989; Searcy and Shaffer, 2011; Messerman et al., 2020). Further, cumulative precipitation is correlated with reproductive investment, with fewer adult females electing to breed in dry years (Trenham et al., 2000). We therefore expected cumulative precipitation to be positively correlated with SCTS larval densities through time. To test this hypothesis, we accessed monthly precipitation data for all study years recorded by a weather station located between the ALT and HAL preserves (Station SRO; CDWR, 2020). We then calculated cumulative precipitation during the adult SCTS emigration period preceding each annual survey (November–February).

2.5. Analysis

To perform all data analyses, we used R software version 4.0.0 (R Core Team, 2020). We calculated relative larval density for each pool by dividing the total number of larvae captured by the number of person-minutes sampled. This response variable was highly zero-inflated due to years when larvae were not detected in a pool, as well as years when pools were dry at the time of sampling. We thus adopted a randomization approach to determine whether observed temporal trends in relative larval densities across preserves were more extreme than those expected from a null randomized distribution.

We began by constructing a general linear mixed model (GLMM) using the *lme4* package (Bates and Maechler, 2010). Relative larval density was the response variable, and we specified predictors of preserve, year, and their interaction, a covariate of wet season precipitation, and an intercepts-only nested random effects structure of pool identity within preserve to account for spatial variation and repeated measures. Due to variation in the number of survey years across preserves and the presence of an interaction term in our model, we examined the Type III sums of squares results using the *car* package (Fox et al., 2012).

Next, we randomized the observed relative larval density data without replacement 1000 times, ran the above-described GLMM on these randomized data, and extracted fixed effect estimates and χ^2 test statistics. To determine whether observed results were more extreme than those from the generated null distribution, we calculated the number of results from the random iterations that exceeded in magnitude the observed value for each fixed effect estimate and χ^2 -value. We then calculated P-values by dividing by 1000.

We determined whether the temporal trend in relative larval densities differed significantly from zero within each individual preserve by running GLMMs with year and wet season precipitation as predictors, pool identity as a random effect, and relative larval density as the response variable for each preserve independently. In the cases of BRN and SWP, where only one breeding pool was present, we instead ran general linear models without the random effect. We followed the same randomization procedure to determine whether the year effect was significant within each preserve. To estimate the magnitude of shifts in larval densities through time, we then calculated the percent change in mean predicted larval densities between the first five years of the study period and last five years of the study period based on the full observed GLMM and each of the preserve-specific models. We also examined trends in when breeding occurred and in total wet season precipitation (see Appendix A) to determine the degree to which either of these variables could account for changes in larval densities.

Correlations between populations (i.e., synchrony) have important implications for metapopulation dynamics, where weak correlations (i.e., greater asynchrony) allow declining populations to be rescued and extirpated populations to be recolonized by dispersers from nearby non-declining populations (Hanski, 1998). We estimated the degree of synchrony in larval densities through time both within preserves and between preserves. To do so, we took 100 random samples of breeding pool pairs from different preserves. Similarly, we took 10 random

samples of breeding pool pairs from each preserve with >1 breeding pool. We calculated Pearson's correlation coefficient (r) for each pool pair, with greater r values representing higher synchrony in larval densities between pools. We removed all replicate pairings, leaving 99 and 38 between- and within-preserve pairs, respectively. To compare synchrony within vs. between preserves, we used a t -test with the r -values as the response variable.

To understand whether preserve characteristics were predictive of temporal trends in relative larval densities through time, we first selected a subset of preserve characteristics that were correlated with each other by $r < 0.7$ (Ratner, 2009). Of the full set of preserve characteristics (Table 1), we selected five: log-number of pools, log-mean pool area, log-Julian date until the last breeding pool at each preserve dried in 2007, length of \geq Low traffic volume roads within 2092-m buffers, and area of suitable habitat within 1850 m of pools. We then extracted the fixed effect estimates of the preserve-by-year coefficients from the full observed GLMM to serve as the response variable. Next, we examined correlations between these eight slopes (representing temporal trends) and the five selected preserve characteristics. Due to the non-normal distribution of the slopes, we employed Spearman's rank correlations for this investigation. For variables that showed a significant correlation with changes in relative larval densities through time, we constructed linear models using all possible combinations of these variables to determine their relative effects on the preserve-specific temporal trends. We used AICc and Akaike weights to identify the best models (Akaike, 1973).

3. Results

Relative larval SCTS densities declined by 48% between the first five years and last five years of the study period, with rates of change differing between study preserves (GLMM randomization; $P_{\text{preserve}} < 0.001$, $P_{\text{year}} = 0.027$, $P_{\text{preserve} \times \text{year}} < 0.001$, $P_{\text{precipitation}} = 0.028$; Table 1; Fig. 2). Mean relative larval densities were the lowest at ALT (Table 1; Fig. 2), where SCTS were introduced, but increased by 175% over the study period (GLMM_{ALT} randomization; observed slope = 0.006, $P < 0.001$). In contrast, larval densities at ENG, HAL, and SWP declined significantly by 63–100% (Table 1; GLMM_{ENG, HAL, SWP} randomizations; slope_{ENG} = -0.03, $P_{\text{ENG}} = 0.006$; slope_{HAL} = -0.007, $P_{\text{HAL}} = 0.006$; slope_{SWP} = -0.11, $P_{\text{SWP}} = 0.037$). Temporal trends in larval densities at BRN, FEM, SCE, and YUB did not differ significantly from zero (GLMM_{BRN, FEM, SCE, YUB} randomizations; $P_{\text{BRN}} = 0.16$, $P_{\text{FEM}} = 0.34$, $P_{\text{SCE}} = 0.40$, $P_{\text{YUB}} = 0.54$), possibly due to the relatively small number of pools at these preserves, but all had negative slopes and predicted declines of 30–100% (Table 1; slope_{BRN} = -0.10, slope_{FEM} = -0.01, slope_{SCE} = -0.02, slope_{YUB} = -0.007). Populations of SCTS at SWP and BRN (each of which feature only one breeding pool) were likely extirpated during the study period despite high initial larval densities (Table 1; Fig. 2).

Relative larval density was positively correlated with annual wet season precipitation. Although the four driest wet seasons occurred during the second half of the study period (2012, 2014, 2018, and 2020; Fig. A1), corresponding with a negative trend in precipitation, this relationship was not significant once the high interannual variation in precipitation was accounted for (linear regression; $R^2 = 0.05$; $P = 0.38$). By including this covariate in the full GLMM, we confirmed that observed declines in relative SCTS larval densities cannot be solely attributed to the negative trend in wet season precipitation. There was also no temporal trend in when peak SCTS breeding activity occurred (linear regression; $R^2 = 0.003$; $P = 0.82$, Fig. A2).

Of the five selected preserve characteristics, only number of pools and Julian date on which the last breeding pool dried at each preserve were significantly correlated with preserve-specific temporal trends in relative larval densities (Table 2). Model selection revealed that the two top-performing linear models included dry date and number of pools, respectively (Table 3). Together, these models accounted for 96% of the

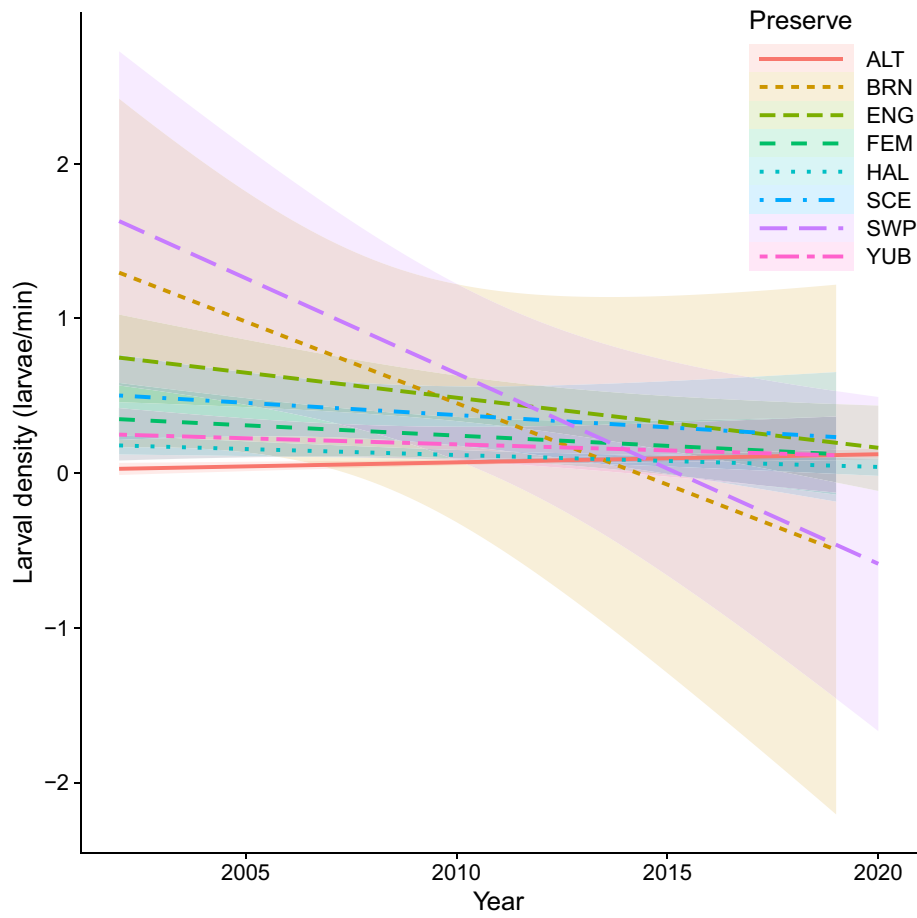


Fig. 2. Preserve-specific trends in relative larval SCTS densities across study years as predicted by the general linear mixed model. Error envelopes indicate 95% confidence intervals for each preserve. Negative estimated mean larval densities suggest SCTS extirpation at BRN and SWP.

Table 2

Spearman's rank correlation coefficients (ρ) and associated P-values between the five selected preserve characteristics and preserve-specific temporal trends in relative SCTS larval densities.

Candidate variable	ρ	P-value
Julian date until dry in 2007	0.87	0.005
Number of pools	0.83	0.011
Length of \geq Low roads in 2092-m buffer	0.67	0.071
Suitable habitat within 1850 m of pools	0.52	0.183
Mean pool area	0.12	0.779

Table 3

Model selection of candidate linear models comprised of the significant predictors of preserve-specific temporal trends in relative SCTS larval densities. All parameters were log-transformed.

Model parameters	df	AICc	Akaike weight	Δ AICc
Julian date until dry in 2007	3	-22.24	0.53	0
Number of pools	3	-21.81	0.43	0.43
Number of pools + Julian date until dry in 2007	4	-17.17	0.04	5.07

total Akaike weight, with a difference of only 10% between them. We thus consider both preserve characteristics to be important predictors of population trends in SCTS. Both preserve characteristics were positively correlated with trends in larval SCTS densities, suggesting that ≥ 2 breeding pools on a preserve (Fig. 3A), at least one of which dries after

28 April even in dry years (Fig. 3B), is associated with substantial improvements in the trend of larval SCTS densities through time.

Larval SCTS densities were largely asynchronous among breeding pools. Although marginally non-significant ($P = 0.058$), mean r was greater within preserves ($\bar{x} = 0.24 \pm 0.32$ SD) than between preserves ($\bar{x} = 0.12 \pm 0.32$ SD). This trend was lost when pairs between ALT and other preserves were removed from the analysis ($P = 0.31$).

4. Discussion

Nineteen years of data collection revealed that SCTS larval densities declined by 48% across remnant habitat patches. While there was a negative trend in precipitation over the course of the study (Fig. A1), this trend was not significant, and the negative temporal trend in SCTS larval densities was significant even after accounting for variable precipitation. The period over which larval densities declined greatly exceeds the average lifespan of the species (6–7 years; Trenham et al., 2000), suggesting that multiple generations of breeding adults have experienced declines in abundance, breeding effort, and/or reproductive success across the seven naturally-occupied study preserves. Any one of these changes would have a negative effect on SCTS population dynamics. Our results indicate that larval density declines were not due to a phenological shift toward earlier breeding and, correspondingly, increased mortality over an extended larval development period prior to sampling (Fig. A2). The population-level declines supported by our findings indicate that current efforts to conserve SCTS on preserves where the species occurred at the time of federal listing in 2003 are inadequate, and that additional management actions are needed for effective SCTS conservation.

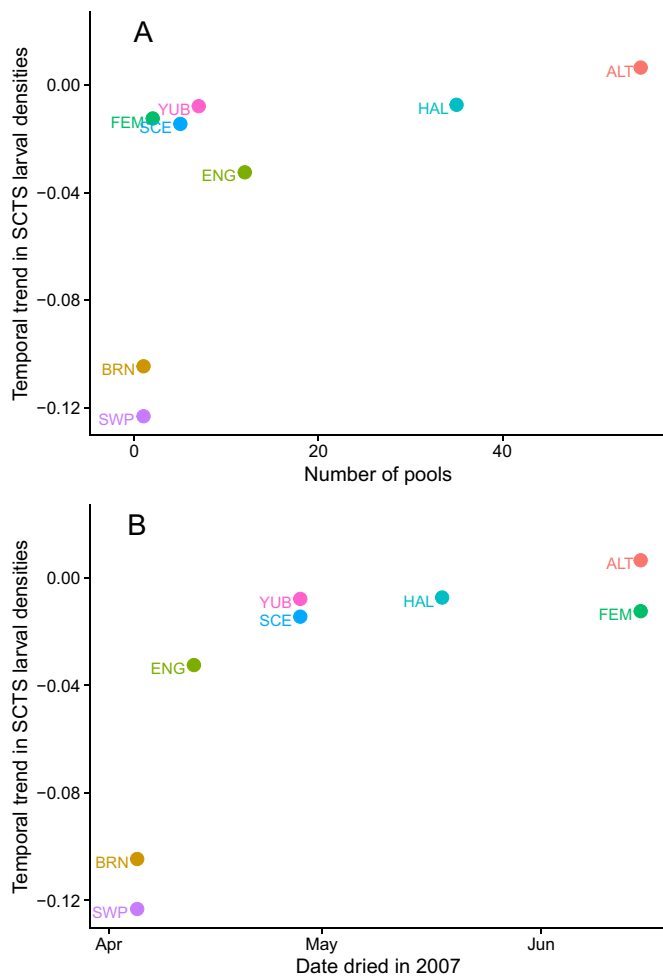


Fig. 3. Preserve characteristics that best predicted temporal trends in SCTS larval densities were (A) number of pools at each preserve, and (B) the maximum date a breeding pool at each preserve held water in 2007.

This study illustrates the importance of managing redundant and resilient populations (i.e., breeding pools) of SCTS for species recovery (Donaldson et al., 2019). The two preserves with only one breeding pool, BRN and SWP, showed the most rapid declines in larval density. It appears likely that SCTS were extirpated from BRN and SWP within the study period, despite relatively high initial larval densities at these study pools (Fig. 2). In contrast, preserves with two or more breeding pools showed much more moderate rates of decline in larval density (Fig. 3A). This result is likely due to recolonization events and rescue effects between local breeding populations, which help to ensure that the SCTS metapopulation at each preserve persists, even as individual breeding pools experience periodic declines or extirpations (Hanski, 1998). A high degree of asynchrony in larval densities between study pools provides a mechanism for local population rescue, underscoring the benefit of providing multiple breeding pools on each preserve to facilitate viable metapopulation dynamics. SWP and BRN also lack a pool with a long hydroperiod, being the two preserves that dried earliest in 2007. More pools on a preserve increase the probability that at least one pool will have a long hydroperiod, but does not guarantee it. For example, ENG has 12 pools, but none of them held water past mid-April in 2007. We found that preserves with at least one breeding pool that held water through 28 April 2007 were likely to have substantially lower rates of decline in larval SCTS densities (Fig. 3B). This dry date serves as a proxy for minimum hydroperiod, given the below-average wet-season precipitation received in 2007 (Fig. A1). Pools with longer hydroperiods have an increased probability of allowing a greater number of

ambystomatid larvae to reach the minimum size required for metamorphosis before pool drying (Pechmann et al., 1989). Further, including breeding pools with longer hydroperiods increases the probability that a metapopulation will experience some recruitment even in drier years, when many local populations experience reproductive failure (Baumberger et al., 2020). Comparable Akaike weights suggest that both the number and dry date of SCTS breeding pools are important predictors of preserve-level trends in larval SCTS densities (Table 3). Future recovery efforts for SCTS should thus work to provide multiple breeding pools (redundancy), with at least one pool having the ability to hold water through the end of April even in dry years (resiliency) on all remnant, restored, and created habitat patches.

Accessible upland habitat is required for terrestrial juvenile and adult survival, which are critical vital rates influencing amphibian population viability (Biek et al., 2002; Vonesh and De la Cruz, 2002; Trenham and Shaffer, 2005). Additionally, breeding pools must be connected by upland habitat for SCTS populations to interact via dispersal events, which may facilitate metapopulation dynamics that enhance viability (Trenham et al., 2001). Upland habitat requirements and movement patterns of SCTS are not well known (but see Cook et al., 2006; Trenham and Cook, 2008), but given that significant portions of SCTS populations elsewhere move 504–1703 m from breeding pools (USFWS, 2016b), it is probable that SCTS upland habitat requirements far exceed the dimensions of even the largest preserve in our study (Table 1). This suggests that habitat outside of preserves is likely essential for SCTS population and metapopulation persistence. However, we found no effect of our upland habitat availability estimate on preserve-specific trends in larval SCTS densities. This unexpected finding may be attributed to inadequate resolution for distinguishing suitable habitat from satellite imagery. Alternatively, upland habitat availability and quality bordering study preserves may have been universally adequate or—more likely given population trends—inadequate for SCTS. In this study, SWP had an order of magnitude less available upland habitat than any other preserve (Table 1), which may have contributed to the apparent extirpation of SCTS at SWP. Given that all other preserves varied by less than three-fold from one another in area, a study across habitat patches with more variable sizes is needed to better evaluate the required upland habitat area for SCTS persistence.

Declines in larval densities across all but one of our study preserves highlight the inadequacy of conserving SCTS only on the remnant habitat patches where they naturally occur. This conclusion is further underscored by our finding that only ALT, where terrestrial habitat was restored, pools were constructed, and SCTS were introduced, showed an increase in SCTS larval densities over the study period (Fig. 2). In addition to high pool redundancy and the presence of a pool with a long hydroperiod, introduced SCTS at ALT may benefit from greater resource availability (e.g., prey or burrows) or fewer predators in a previously unoccupied habitat, population augmentation by a secondary introduction of breeding adults, and/or genetic effects of introduction of unrelated breeders (i.e., hybrid vigor; Fitzpatrick and Shaffer, 2007). Whatever the causal links, increasing larval densities at ALT, paired with our findings that SCTS do better under preserve conditions that facilitate metapopulation viability, indicate promising paths toward more effective SCTS conservation.

Results of this study suggest that management actions wherein SCTS are introduced or reintroduced to sites featuring multiple breeding pools of sufficient hydroperiod surrounded by suitable upland habitat may result in additional viable SCTS metapopulations. Given current low connectivity between our study preserves, our findings further indicate that the establishment of new SCTS breeding populations within and between currently occupied preserves, paired with efforts to improve overall connectivity across the network of SCTS habitat patches such that metapopulation dynamics are fostered, will likely improve conservation outcomes for SCTS. Rapid rates of development on the Santa Rosa Plain suggest that such actions should be taken quickly, before potential habitat patches and corridors are lost from the landscape. It

will also remain important to conserve SCTS by improving existing habitat. For example, hydroperiod may be optimized for extant breeding pools by increasing pool depth and/or soil compaction and reducing vegetative growth (e.g., through grazing; Pyke and Marty, 2005). Further research is also needed to identify the appropriate density of pools for optimal SCTS management. While results indicate that greater redundancy of breeding sites leads to more favorable population trends, there must be some pool density at which terrestrial habitat becomes limiting and further pool creation will cause populations to decrease. This is particularly likely given the large terrestrial habitat requirements of CTS (Searcy and Shaffer, 2011).

The observed declines across preserves were not primarily due to the negative trend in cumulative precipitation (Fig. A1), as interannual variation in winter precipitation was corrected for in the statistical model. The system of preserves in Sonoma is thus falling short for SCTS recovery even before factoring in the negative predicted effects of climate change. Under climate change, California is predicted to experience increasing temperatures and less predictable precipitation patterns (Vaghefi et al., 2017). These conditions are expected to result in a higher frequency of drought, leading to interrupted and/or shortened pool hydroperiods (Brooks, 2009). It follows that SCTS populations are likely to experience further increases in the frequency of reproductive failure, consistent with patterns described in other pool-breeding amphibian species (Daszak et al., 2005; McMenamin et al., 2008; Westervelt et al., 2013). To mitigate the negative consequences of climate change, our findings suggest that created and restored ephemeral SCTS breeding pools should be designed to hold water through late April even in dry years. This strategy should safeguard against years in which metapopulations experience complete reproductive failure, improving the likelihood of SCTS persistence on the Santa Rosa Plain.

The life history of SCTS and threats faced by this endangered salamander are comparable to those of many biphasic pool-breeding amphibians. We thus expect that the preserve design features shown to be most effective by our results (i.e., each comprising multiple breeding populations including at least one with sufficient hydroperiod to support recruitment during drought years) are likely to broadly benefit pool-breeding amphibian conservation efforts. Though the importance of hydroperiod and inter-pool connectivity for pool-breeding amphibian population and metapopulation viability is well-established (reviewed in Semlitsch, 2000), few studies have empirically demonstrated the value of these guidelines for enhancing pool-breeding amphibian conservation at the preserve scale (but see Rannap et al., 2009). Due to the variable nature of amphibian population dynamics (Marsh, 2001), it was only with a very extensive dataset (both spatially and temporally) that we were able to discern these patterns.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary analysis and figures

Supplementary analysis and figures to this article can be found online at <https://doi.org/10.1016/j.biocon.2021.109320>.

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