| 1 | Title: Saving all the Pieces: | an Inadequate Conservation Strategy for an Endangered |
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| 2 | Amphibian in an Urbanizing | g Area |
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40 Title: Saving all the Pieces: an Inadequate Conservation Strategy for an Endangered

41 Amphibian in an Urbanizing Area

42

43 Abstract

The Sonoma California tiger salamander (SCTS) is a federally endangered vernal pool-breeding 44 distinct population segment and the subject of conservation efforts consisting primarily of 45 protecting existing populations in remnant habitat patches—preserves—in a rapidly urbanizing 46 landscape. We conducted a 14 year (2002 – 2015) study of SCTS breeding activity at 112 pools 47 48 on eight preserves encompassing all protected SCTS breeding sites at the time of federal listing in 2003. We used timed dignet surveys to measure relative density of SCTS larvae in preserve 49 50 breeding pools, and validated our results with exhaustive box enclosure sampling, which 51 allowed us to estimate absolute larval abundance from dipnet data. Our surveys show a large 52 decrease in total SCTS larval abundance and number of pools used for breeding at preserves 53 where SCTS are naturally occurring. Larval abundance was highly variable across years, with 54 variability inversely correlated with preserve size and number of pools. The decline in larval abundance, likely indicative of a rapidly shrinking population, appears to result from habitat 55 loss and fragmentation associated with urbanization, increasingly dry conditions over the study 56 57 period, and mostly non-native vertebrate predators in some deeper breeding pools. Drier 58 conditions predicted to accompany climate change are likely to further depress future larval 59 production. In contrast to overall declines in naturally occurring SCTS, larval production 60 increased at the one study preserve where the SCTS population was introduced and

| 61 | augmented, raising the possibility of successful SCTS conservation through active conservation |
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| 62 | interventions. Our results suggest that a conservation strategy of preservation of remnant |
| 63 | habitats and populations is unlikely to successfully conserve SCTS, which appears to be one of a |
| 64 | growing number of conservation-reliant species requiring ongoing active conservation |
| 65 | management to avoid extinction. |
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76 Introduction

Efforts to conserve imperiled and declining species typically give greatest emphasis to 77 78 preserving habitat remnants where the species still persists (Possingham et al., 2015). Success 79 of this approach requires protection of enough habitat to support populations that can 80 withstand the stochasticity inherent in genetic, population, and environmental processes (Lande, 1993; Soule & Simberloff 1986). Variation in habitat quality and specialized 81 82 requirements of the species of concern, including in some cases the need for more than one 83 type of habitat (Rodewald, 2015), complicate the requirements for conservation success. Additional challenges are expected in the future with continuing degradation of the matrix in 84 which protected habitat patches are located (Watling et al., 2011), and climate change and the 85 interactions of climate change and habitat loss and fragmentation (Brook et al., 2008; Mantyka-86 87 Pringle et al., 2015).

Given these challenges, the effectiveness of conserving species through preservation of habitat 88 89 remnants with relict populations cannot be assumed. Ongoing assessment of conservation 90 performance, including population trends of taxa of concern, is essential (Gerber et al., 1999; 91 Martin et al., 2007). Absent such assessment, failure of this strategy may not be evident before 92 alternatives are no longer available or populations have declined to unrecoverable levels (VanderWerf et al., 2006), i.e., extinction debt (Kuussaari et al., 2009). Furthermore, with the 93 growing prevalence of conservation-reliant species (sensu Scott et al., 2005), information 94 95 produced through such assessments is needed for the active management required for 96 recovery of many species (Braverman, 2015).

97 Amphibians, the most threatened class of vertebrates (Stuart, 2004; IUCN, 2015), present a 98 particularly complex conservation challenge, as habitat loss and fragmentation is the greatest 99 threat to the group (Cushman, 2006), and many species require both aquatic and terrestrial 100 habitat, as well as movement corridors between those habitats (Pittman et al., 2014). In areas 101 of intense landscape conversion such as urbanizing areas, in addition to outright loss of aquatic 102 and terrestrial habitats (Houlahan and Findlay, 2003; Rubbo and Kiesecker, 2005), amphibians 103 may be reduced to small, isolated habitat patches in a matrix of hostile land uses (Semlitsch and 104 Bodie, 1998), leading to genetic (Titus et al., 2014) and demographic (Pickett et al., 2014) 105 hazards of small populations, impaired metapopulation function (Heard et al., 2012), and 106 reduced habitat quality (Riley et al., 2005; Rubbo and Kiesecker, 2005). Furthermore, 107 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) 108 109 and barriers (e.g., roads; Gibbs and Shriver, 2005) are likely to severely constrain their resilience 110 in response to future climate change (Wilson et al., 2013). 111 The Sonoma County California tiger salamander (SCTS) is a distinct population segment of the California tiger salamander (Ambystoma californiense; CTS; Shaffer et al., 2004), a federally 112 113 protected pond-breeding species endemic to the lowlands of California. SCTS, listed as 114 endangered under the federal Endangered Species Act in 2003 (USFWS, 2003), occurs

exclusively in vernal pools and nearby terrestrial habitats in a small portion of the Santa Rosa

116 Plain and adjacent lowlands, a rapidly urbanizing area north of San Francisco.

Habitat loss is the leading threat to CTS generally (Davidson et al., 2002; Fisher and Shaffer,
1996), and 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, 2014). As of
1994, vernal pool habitat on the Santa Rosa Plain was estimated to have decreased by more
than 85% from its historical extent (Patterson et al., 1994). Currently, approximately 7,000 –
8,000 ha of potential SCTS habitat remains, most of it highly fragmented (USFWS, 2014).

124 Since the population's listing, SCTS conservation efforts have focused primarily on protection of existing populations at preserved remnant habitat patches—preserves—in the suburban/rural 125 matrix (USFWS, 2005; 2014). Because of continued expansion of human activities, SCTS habitat 126 127 available for preservation is increasingly scarce and fragmented (Cook et al., 2006; USFWS, 128 2014). As conservation options become foreclosed, it is important to know whether the current 129 remnant population approach to SCTS conservation is effective, whether it is likely to be effective in the future, and how it can be made more effective. A difficulty in answering these 130 131 questions is that because of the highly variable nature of CTS population dynamics (Trenham et al., 2000), long-term study is necessary to discern population trends. Until now, such long-term 132 133 information was not available.

This study uses a 14-year record (2002 – 2015) of SCTS larval surveys at preserves on the Santa
Rosa Plain to assess the effectiveness of current SCTS conservation efforts. Our eight study
preserves comprise all of the known protected locations of SCTS breeding populations at the
time of the population's listing (USFWS 2005). Seven of the eight preserves host remnant

naturally occurring populations of SCTS; the eighth is a restored site where SCTS were
introduced. We assess trends in SCTS breeding activity at these preserves, examine factors that
favor breeding success, and provide an outlook for SCTS in the face of predicted climate
change.

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143 CTS breeding biology

CTS adults migrate to vernal pools during substantial rainfall events from November through 144 February (Loredo and Van Vuren, 1996). They remain in the pools to breed for up to several 145 146 weeks before moving to upland habitats where they spend most of the year underground in small mammal burrows. Aquatic larvae emerge approximately two weeks after eggs are 147 148 deposited. Following a minimum post-hatching development period of 10 weeks, surviving 149 larvae metamorphose and move to upland habitats (Jennings and Hayes, 1994). Continuous 150 pool hydration during the entire egg and larval development period is required for production 151 of metamorphs.

The activities of CTS in their upland habitat are poorly understood and the distance SCTS move from their breeding pools is unknown. Studies of CTS elsewhere indicate substantial movement (Trenham and Shaffer 2005, Orloff 2011, Searcy et al. 2013). The most recent trapping study of the species estimated that 95% of CTS were located within 1850 m of their breeding/natal pool (Searcy et al. 2013).

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159 Methods

160 Study Area

Our study area consisted of eight preserves, lands protected from development for the purpose 161 162 of maintaining plant and wildlife habitat, on the Santa Rosa Plain, Sonoma County, California (38.45° N, 122.70° W; Fig. 1). Study preserves range in area from 1.2 ha (SWP) to 69.6 ha (HAL; 163 Table 1). All preserves include upland habitat dominated by a mix of native and non-native 164 grasses and forbs, and from one (SWP and BRN) to 49 (ALT) vernal pools. The longest-persisting 165 166 pools hold water until June in wetter years. Three preserves, ENG, ALT, and YUB, include human-constructed pools added as mitigation for the loss of natural wetlands and designed to 167 mimic natural vernal pools (DFG, 2003). SCTS is naturally occurring at all preserves except ALT, 168 169 which was stocked with SCTS larvae in 1996 (C. Patterson, personal communication) and adults 170 in 2004 (W. Cox, personal communication).

171 Larval Surveys

To determine relative SCTS larval density at study pools, we conducted standardized dipnet
surveys (Heyer et al., 1994) in March of each year from 2002 to 2015 (Table 1). Surveys were
timed to occur after larvae had reached a detectable size and before any larvae had
metamorphosed, based on observed rain events and SCTS breeding migration activity in that
year (Cook et al., 2006). Survey coverage varied by preserve (Table 1). With minor exceptions
(Table 1), all pools at four preserves (HAL, ENG, SWP, and ALT) were sampled in all years of the

study. Both pools at FEM were sampled in all years except 2011. The other three preserves

179 (BRN, SCE, YUB), were sampled for fewer years, primarily early in the study period.

We surveyed for larvae by sweeping standard "D" shaped dipnets along the pool bottom and 180 through the water column, sampling all aquatic habitat types in each pool (i.e., deep to shallow 181 182 open water, and emergent and floating vegetation). Two-to-twelve surveyors sampled each pool. All were trained in the field by the same person (D.G.C.) to ensure consistency. We timed 183 184 surveys to allow calculation of capture rate per unit effort. Sampling duration varied with pool 185 size (\bar{x} = 34.6 person minutes per pool, sd = 31.6, n = 764 pool surveys). We identified all larval amphibians and other vertebrates captured to species, recorded number of SCTS larvae, and 186 released all larvae at the point of capture after completion of the pool survey. We measured 187 188 the maximum water depth of each pool immediately after sampling.

At the time of the 2007 survey, we visually located the transition between hydrophytic and upland-dominated vegetation around each pool and used Trimble GeoExplorer 3 hand-held GPS units to map the pool perimeters. The GPS data were entered into a GIS (ESRI, 2002) from which pool areas were calculated. In 2007, we also monitored study pools weekly after our larval survey to determine date of drying.

194 Analysis

We calculated relative larval density for each pool by dividing the total number of larvae
captured by the number of person-minutes sampled. To determine larval productivity of pools,
we calculated an SCTS larval abundance index for each pool in each year by multiplying the

larval density value by pool volume, estimated as ½ maximum pool depth in the survey year
times pool area. We calculated a preserve larval abundance index each year by summing the
abundance values for all pools in the preserve.

In 2015, we used Google Earth GIS to determine the area of contiguous potential SCTS upland
habitat around each study preserve. We defined potential upland habitat as undeveloped, rural
residential, agricultural, or preserve lands that were within 1850 m of the preserve (Searcy et
al. 2013) and not separated from the preserve by a barrier (e.g., major road or incompatible
development).

206 To characterize moisture conditions during the SCTS breeding season, we used total

207 precipitation minus evapotranspiration from November through February, recorded at a

208 California Department of Water Resources weather station located between the ALT and HAL

209 preserves. Evapotranspiration was determined using CIMIS Penman and Penman-Monteith

210 equations and weather data measured over a well-watered reference surface (California

211 Department of Water Resources, 2015). For all analyses, statistical methods follow Zar (1998);

all statistical tests were carried out in SPSS 23 (IBM, 2015).

213 Box sampling for estimating larval abundance

To assess the reliability of our dipnet-derived abundance index, in 2015 we exhaustively
 sampled a stratified random array of 1 m² enclosed plots at 13 study pools (Heyer et al., 1994).
 We randomly located transects across pools (Cook and Jennings, 2007) and sampled plots at 3

217 m intervals along each transect. Number of transects and plots varied, depending on pool size

218 (transects: n = 132, $\bar{x} = 10.1$ per pool, sd = 4.0; plots: n = 408, $\bar{x} = 31.4$ per pool, sd = 15.4).

The sample plot enclosure consisted of a 1.0 m² open-ended plywood box that we pressed into the pool substrate. We systematically sampled the water enclosed by the box in six successive dipnet sweeps, each of which sampled the entire enclosure. All SCTS larvae captured in each sweep were counted and, following the sixth sweep, released. Proportion of pool area sampled ranged from 3.2% to 16.3% ($\bar{x} = 6.5\%$, sd = 3.4). The day after box sampling, the pool was resurveyed using our standard timed dipnet survey method.

At each box sample plot we measured the water depth at the center of the plot. Mean box sample water depth ($\bar{x} = 13.5$ cm, sd = 6.2, n = 13) at the 13 sampled pools did not differ significantly from our standard measure of mean pool depth ($\frac{1}{2}$ maximum measured depth; $\bar{x} =$ 12.4 cm, sd = 8.1; paired *t*-test, t = 1.12, df = 12, p > 0.25, and the two measures were strongly correlated ($r^2 = 0.85$; $F_{1,11} = 60.1$, p < 0.001), indicating that $\frac{1}{2}$ maximum pool depth reliably approximated mean pool depth and could be used, with pool area, to estimate pool volume.

We captured a total of 391 SCTS larvae in the box samples, the proportion captured declining with each sweep, from 39% (n = 149) on the first sweep to 2% (n = 8) on the last. Capture rates by sweep fit a negative exponential function ($y = 327.11e^{-0.58x}$, $r^2 = 0.95$); a projection based on this model suggests that fewer than 3% of larvae were not captured. We conclude that the box samples closely estimate numbers of larvae in the box. As the box surveys representatively sampled a known proportion of each pool, the box survey provides an unbiased estimate of total number of larvae present in each pool. Larval abundance indices derived from the dipnet

surveys at the 13 box-sampled pools were highly correlated with the box sample results (Fig. 2),
indicating that the larval abundance index based on dipnet surveys is a reliable index of actual
larval abundance.

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242 Results

Timed dipnet surveys at the three preserves (ENG, HAL, and SWP) with naturally occurring SCTS 243 sampled each year over the entire study period indicate that total SCTS larval abundance 244 declined substantially from 2002 - 2015 (Fig. 3a), with statistically significant declines at two of 245 246 the three individual preserves and near-significant declines at the third (Fig. 3b). No larvae were detected at SWP for the last five years of the study. Total number of pools with larvae also 247 declined significantly (Figures 4a & b). The one preserve where number of pools with larvae did 248 249 not decline (ENG) included five constructed pools built three years prior to our study. Spread of SCTS to these new pools likely increased the number of active pools over the study period. 250

A fourth preserve (FEM), surveyed in 13 of the 14 years, showed a non-significant tendency for declining larval abundance and a significant decline in number of pools where larvae were detected (Fig. 5). Larval abundance at FEM in 2010 was anomalously high, the greatest abundance of any preserve in any year.

The remaining preserves with naturally occurring SCTS were sampled for substantially shorter periods, primarily in the early years of the study. One of these preserves (BRN) showed a significant decline in larval abundance ($F_{1,7}$ = 10.68, r^2 = 0.60, p < 0.02). The other two (SCE and

YUB) showed no trend (SCE: $F_{1,6} = 0.02$, p > 0.80; YUB: $F_{1,7} = 0.06$, p > 0.80). Collectively, these three preserves accounted for a small proportion ($\bar{x} = 8.5\%$, sd = 4.8) of total larval abundance among all preserves (Table 2).

Larval abundance was highly variable (Figures 3 - 5), and was more than 20 times greater in the
 most productive years (2002 and 2004) than in the least productive (2007, and 2012; Fig. 3a).
 Among the four preserves with naturally occurring SCTS sampled most consistently, larval
 productivity was more variable at smaller preserves with fewer pools (coefficient of variation:
 SWP > FEM > ENG & HAL; Table 2).

The mean proportion of preserves' pools that were active was inversely correlated with number of pools at the preserve (eight preserves: $F_{1, 6} = 15.88$, p < 0.01, $r^2 = 0.73$; excluding SWP, $F_{1, 5} =$ 12.00, p < 0.02, $r^2 = 0.71$). At preserves with seven or more pools (ENG, HAL, YUB, ALT), fewer than half of all pools were active on average (Table 2).

270 In contrast to the seven preserves with naturally occurring SCTS, the ALT preserve showed a 271 significant increase in both larval abundance and number of pools with larvae (Fig. 6). In the 272 first three years of the study, SCTS larvae occurred only in the single deep pool where they were introduced. Although larvae were found at an increasing number of pools in succeeding 273 years, the vast majority (\bar{x} = 88%, sd = 13.7, range = 61 – 100) of larval production at ALT 274 continued to occur in the two deepest pools, a proportion that remained high (\bar{x} = 85%, sd = 275 276 13.3, range = 63 - 100) in the last six years of our study, when an average of six pools per year 277 were active.

Among all pools sampled each year from 2002 – 2015 where SCTS are naturally-occurring, larval 278 279 density was higher in years of greater moisture during the breeding season (Fig. 7). Proportion 280 of pools with larvae present and mean larval density at pools with larvae (i.e., excluding pools without larvae) were also greater in years of greater moisture (% active pools: $F_{1.12}$ = 9.60, p <281 282 0.01; larval density at active pools: $F_{1,12}$ = 4.95, p < 0.05), indicating that in dry years not only were fewer pools used for breeding, but fewer larvae were present at those pools that were 283 active. Water availability during the breeding season, like larval densities, declined significantly 284 285 over the 2002 – 2015 period, and was below the 14 year mean (\bar{x} = 38.9 cm, sd = 4.8) in all of 286 the last four years ($\bar{x} = 22.9 \text{ cm}$, sd = 6.1; Fig. 7).

Our monitoring of pool drying dates in 2007 showed that duration of pool hydration was 287 strongly correlated with depth at time of survey ($r^2 = 0.87$, p < 0.001). In addition to more 288 289 frequently providing sufficient water for SCTS breeding, deeper pools supported greater average larval density, but only if they were predator-free (Fig. 8a & b). We observed four CTS 290 291 aquatic macropredators at study pools: red swamp crayfish (Procambarus clarkii), mosquitofish 292 (Gambusia affinis), green sunfish (Lepomis cyanellus), and threespine stickleback (Gasterosteus 293 aculeatus). All except stickleback are non-native species. These predators were detected at 11 294 study pools at HAL, ENG, FEM, SCE, and YUB, and were significantly more likely to occur in 295 deeper pools (Fig. 8c).

296

297 Discussion

298 Our 14-year study indicates that SCTS breeding activity has decreased precipitously, likely 299 indicating a rapid decline in the population since it was federally listed in 2003. Timed dipnet 300 survey results, validated by box sample data, showed sharp decreases in total SCTS larval 301 abundance and number of pools used for breeding at preserves where SCTS are naturally 302 occurring. Although larval production increased in an introduced SCTS population (ALT; see 303 below), total production at all preserves surveyed in 2015 (including ALT) was less than 20% of the total at the beginning of our study. Declines were steepest at SWP, where SCTS may have 304 305 become extinct during the study. We conclude that current SCTS conservation measures are 306 insufficient to maintain a viable population.

307 Habitat loss and fragmentation is the leading threat to amphibians (reviews in Cushman, 2006; 308 Hamer and McDonnell 2008), and pond-breeding salamanders, with their high demographic 309 stochasticity and heavy reliance on dispersal for frequent population rescue, are particularly 310 vulnerable (Green, 2003). The patterns of SCTS decline we observed are consistent with these generalizations. The preserves in our sample are small, isolated patches of remnant habitat 311 312 located in areas of recent and ongoing land conversion. Among consistently sampled preserves with naturally occurring SCTS, both rate of decline of larval abundance and its variability, a 313 314 population risk factor (Trenham et al., 2000), were greatest at the smallest, most isolated 315 preserve (SWP), and were lowest at the largest, least isolated preserves. Significantly, however, 316 even the biggest preserve (HAL) showed a large decline.

Amphibian studies have increasingly emphasized the need to accommodate species' terrestrial
life stages (Quesnelle et al., 2015; Trenham and Shaffer, 2005). 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 CTS populations elsewhere disperse 630 m
(Trenham and Shaffer, 2005) to 1850 m (Searcy et al., 2013) from breeding pools, and possibly
farther (Orloff, 2011), it is probable that SCTS upland habitat requirements far exceed the
dimensions of even the largest preserve (70 ha) in our study, meaning that habitat outside of
preserves is essential for population persistence.

325 Conversion of grasslands and low intensity agricultural lands to residential, commercial, and 326 intensive agricultural land uses has reduced SCTS habitat around preserves in recent decades (Patterson et al., 1994; USFWS, 2014). Conversion has been most complete around SWP, where 327 328 more than 98% of surrounding habitat has been eliminated (Stokes et al., 2008). Areas around 329 preserves have also become increasingly hostile to SCTS, with proliferation of barriers (e.g. 330 roads and curbs) and novel mortality agents (e.g. storm drains and vehicle traffic). Substantial 331 mortality of SCTS crossing roads during winter rainstorms has been observed since 2000 332 (D.G.C., unpublished data; USFWS, 2014).

Despite these losses, the area of remaining habitat around most study preserves (Table 1) still exceeds the hypothesized lower size limit (850 – 1100 ha) for CTS viability (Searcy et al., 2013, USFWS, 2014). Nonetheless, we observed declines of SCTS at the preserves with the largest areas of surrounding habitat. These declines occurred despite the designation, since 2003, of additional protected areas within dispersal range of our study preserves (USFWS, 2014). Thus, merely preserving habitat "as is" appears to be insufficient to reverse SCTS decline. Reduction

of novel mortality agents and barriers, along with enhancement of habitat quality, may also benecessary.

In addition to habitat loss, the increased frequency of dry winters appears to have contributed 341 to SCTS decline, as indicated by the correlation between larval abundance and seasonal 342 343 moisture, and the concentration of larval production in deeper pools, as long as predators are 344 absent. Drought has large negative effects on other pond-dependent amphibians (Hossack et al., 2013; Mac Nally et al., 2009; Walls et al., 2013). Besides providing favorable conditions for 345 346 breeding in dry years, deeper pools retain water for a longer period in spring, allowing more time for larvae to metamorphose. We expect that reduced metamorph production adds to the 347 negative effect of drought on larvae production, making deep pools even more important for 348 349 SCTS persistence than our results suggest. Management measures such as constructed pools to 350 increase population connectivity and increased pool depth to enhance pool persistence may 351 reduce these effects (Scheele et al., 2012). The negative correlation we observed between number of pools at a preserve and the proportion used for breeding, suggests that additional 352 353 pools would primarily enhance SCTS larval production at preserves with few pools where SCTS 354 may be pool-limited. Deeper pools, however, would likely increase larval production at all 355 preserves, at least in dry years (Cook et al., in preparation).

Predacious fish and crayfish, also appear to be depressing SCTS larval production. Probably arriving during winter floods that temporarily connect pools with perennial streams, these mostly non-native predators occur mainly in deeper pools, reducing their value for SCTS breeding. Sensitivity to introduced aquatic predators is well documented in amphibians

(Bucciarelli et al. 2014), including ambystomid salamanders (Maurer et al. 2014). Introduced
fish may pose an especially serious threat in urbanizing areas (Hamer and McDonnell 2008),
where introductions are more likely (Copp et al. 2005) and pool hydrology may be altered to be
more conducive to fish persistence (Rubbo and Kiesecker 2005).

As in other amphibian species (Hof et al., 2011; Wilson et al., 2013), multiple factors—in this 364 365 case habitat loss and fragmentation, unfavorable hydrologic conditions, and predators—appear 366 to be responsible for SCTS decline. These factors may interact synergistically (Brook et al., 367 2008). For example, drier conditions favor breeding in deeper pools, which are more often inhabited by predators and thus may be ecological traps (Battin, 2004). Similarly, a possible 368 adjustment to less favorable weather conditions is greater movement; however deteriorating 369 370 matrix conditions around SCTS habitats are likely to prevent movement (Watling et al., 2011) or 371 increase mortality during movement (Gibbs and Shriver, 2005).

372 Future climate change

Climate projections indicate that temperatures across California will rise 1 - 3° C by 2050,
exceeding the global rate of warming over recent decades (Cayan, 2008; 2009). Future
precipitation trends are less certain. Most models predict declining rainfall and high interannual variability (Cayan, 2009), increasing the likelihood of drought (Mastrandrea and Luers,
2012). Uncertainty regarding future precipitation trends notwithstanding, however, increased
evapotranspiration associated with higher temperatures alone is expected to cause drier
conditions and shorter pool hydroperiods (Matthews, 2010).

While the effects of climate change on amphibian larval production are likely to be complex (O'Regan et al., 2014), the observed correlation between SCTS larval production and seasonal moisture, and the extremely low larval production in dry years, suggest that future climate change poses a serious threat to SCTS. With additional drying, functional breeding pools will be fewer and less frequently available, and those that hold water of sufficient depth for breeding will dry sooner, reducing production of larvae and metamorphs, which is likely to amplify recent population declines.

Species are expected to shift their ranges in response to climate change, and such range shifts have already been documented in diverse taxa (Parmesan, 2006). However, given its limited vagility, specific habitat requirements, the disjunct nature of its native range, and the highly fragmented condition of its habitat, SCTS is unlikely to be able to move to more suitable locations. If SCTS is to persist through projected climatic changes, conservation planning that responds to climate change, and active management of habitat and populations, will be required (Robillard et al., 2015).

394 Potential for conservation success: ALT Preserve

In contrast to the widespread pattern of decline across preserves where SCTS naturally occur, larval production increased substantially at ALT, a restored site where SCTS were introduced and the population was later augmented. SCTS breeding at ALT increased to the point that by 2013, annual larval production there exceeded that of all other surveyed preserves combined (although total production was far below levels in the early years of the study).

A possible explanation for the contrary trend at ALT is the presence of unusually deep and long-400 401 persisting pools that, unlike most deep pools at other preserves, are predator free and therefore are more favorable for production of larvae as well as metamorphs that can 402 403 ultimately recruit to the breeding population. Alternatively, SCTS at ALT may benefit from 404 greater resource (e.g., food or estivation sites) availability in a previously unoccupied habitat, numerical effects of breeding by translocated adult salamanders, and/or genetic effects of 405 introduction of unrelated breeders (hybrid vigor; Fitzpatrick and Shaffer, 2007). Regardless of 406 407 its cause(s), the increase of SCTS at ALT indicates the possible value of active restoration 408 measures (Possingham et al., 2015) such as translocation, although given the risks of such 409 measures (Germano et al., 2015), they should be pursued with caution.

410 *Conservation reliance*

411 Our results suggest that SCTS is one of a growing number of conservation-reliant species (Goble 412 et al., 2012), which depend on ongoing active management for persistence. Current efforts to 413 conserve SCTS through protection of remnant populations and habitat patches in the species' 414 native range appear to be failing, likely due to a combination of interacting threats including 415 ongoing habitat loss and fragmentation outside of preserves, increasingly unfavorable 416 hydrologic conditions, and presence of predators, mostly non-native, in breeding pools. As a 417 relatively long-lived species (> 10 years; Trenham et al., 2000), SCTS at some preserves may already be in a state of extinction debt. 418

The increase in larval abundance at the preserve where SCTS were introduced suggests the
 possibility of conservation success through interventions beyond preservation of remaining

| 421 | habitat. Promising interventions include enhancement of terrestrial habitat quality, threat |
|-----|-----------------------------------------------------------------------------------------------|
| 422 | reduction and management in habitats around preserves, addition of constructed pools at |
| 423 | preserves with few pools, addition of deeper pools, aquatic predator prevention and control, |
| 424 | and translocation of adults and larvae. Many of these measures are largely untested for CTS, |
| 425 | and an adaptive management approach is warranted. With projected increasing future impacts |
| 426 | of climate change and human alteration of habitats worldwide, SCTS's dependence on active |
| 427 | conservation management for persistence likely exemplifies a conservation future that will be |
| 428 | the new normal for many species. |

431 Acknowledgements

| 432 | This study would not have been possible without field assistance from Jon Edwards, Natalie |
|-----|-------------------------------------------------------------------------------------------------|
| 433 | Graham, Kathleen Grady, Bill Cox, and many other volunteers. We thank David Kelly, Stacy |
| 434 | Martinelli, Stephanie Buss, and Harvey Rich for supporting this project. This study was funded, |
| 435 | in part, by a grant from USFWS (F13AP00010). All field work was conducted under permit from |
| 436 | California Department of Fish and Wildlife (SCP-514) and USFWS (TE816187). USFWS-approved |
| 437 | procedures to prevent the spread of amphibian diseases were followed during all surveys. |

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| - | | | | Preserve | | | | | |
|---------------------------------------|---------|---------|---------|------------|---------|----------------------|-------------|---------|---------------------|
| Characteristic | ENG | HAL | SWP | FEM | BRN | SCE | YUB | ALT | Total |
| Area (ha) | | | | | | | | | |
| Preserve | 16.2 | 69.6 | 1.2 | 32.0 | 5.3 | 9.3 | 4.9 | 18.2 | 156.6 |
| Potential habitat ^a | 1660.2 | 1203.8 | 20.9 | 863.6 | 905.4 | 664.0 | 1067.8 | 1175.2 | 4820.3 ^b |
| Breeding pool | 1.18 | 1.90 | 0.67 | 3.06 | 0.16 | 0.24 | 0.53 | 0.94 | 8.68 |
| Number of pools | | | | | | | | | |
| All | 12 | 35 | 1 | 2 | 1 | 5 | 7 | 49 | 112 |
| Breeding pools | 10 | 16 | 1 | 2 | 1 | 4 | 4 | 12 | 50 |
| Mean pool depth (cm) 2002-2008, 2010 | | | | | | | | | |
| Breeding pools | 23.0 | 26.2 | 56.0 | 71.8 | 24.5 | 41.8 | 32.4 | 33.4 | |
| Most productive pool ^c | 34.3 | 38.8 | 56.0 | 49.8 | 24.5 | 29.8 | 37.4 | 86.3 | |
| Mean dry date in 2007 (Julian day) | | | | | | | | | |
| Breeding pools | 95.7 | 102.0 | 95.0 | 152.0 | 95.0 | 104.3 | 104.3 | 110.9 | |
| Most productive pool | 95 | 123 | 95 | 138 | 95 | 95 | 109 | 166 | |
| Survey years | 2002-15 | 2002-15 | 2002-15 | 2002-15 | 2002-10 | 2002-10 ^d | $2002-10^d$ | 2002-15 | |
| | | | | except 201 | L | | æ 2014 | | |

Table 1. Study preserves and years surveyed, 2002 - 2015, Santa Rosa Plain. Breeding pools are pools in which we detected SCTS larvae at least once during the study.

^a The area of contiguous undeveloped land including preserve and area within a 1.85 km radius (Searcy et al., 2013) of the preserve without major isolating barriers (i.e., the area of habitat potentially accessible to SCTS at the preserve).

^b Total area is less than the sum of individual values because surrounding habitat areas of individual preserves overlap.

^c Pool in preserve with greatest mean larval abundance over the comparison period (2002-2008, 2010).

^d In 2009, a year of late rainfall, five pools at SCE, and YUB only sampled for presence/absence of larvae/eggs to avoid disturbing SCTS eggs.

| | | | | Preserve | | | | | |
|-------------------------------------------------------------------|--------|-------|-----------------|--------------|-------|-----------|--------------------|---------|---------|
| | ENG | HAL | SWP | FEM | BRN | SCE^{a} | \mathbf{YUB}^{a} | ALT^b | Total |
| Mean annual relative | | | | | | | | | |
| larval abundance ^c | | | | | | | | | |
| 2002-2015 | 2118.4 | 555.4 | 1048.8 | 2336.5^{d} | | | | 1218.3 | 7277.4 |
| 2002-08, 2010 | 3169.3 | 845.6 | 1835.5 | 3705.6 | 192.3 | 248.8 | 486.0 | 880.5 | 11363.6 |
| Coefficient of Variation (sd/\bar{x}) , annual larval abundance | | | | | | | | | |
| 2002-2015 | 1.05 | 1.01 | 1.89 | 1.42^{d} | | | | 0.99 | |
| 2002-08, 2010 | 0.78 | 0.71 | 1.30 | 0.98 | 1.10 | 0.76 | 0.74 | 1.32 | |
| Mean annual % active pools | | | | | | | | | |
| 2002-2015 | 47 | 37 | 43 ^e | 77^d | | | | 9 | |
| 2002-2010 | 42 | 19 | 67 | 89 | 78 | 53 | 32 | 7 | |
| No. of years with no larvae | | | | | | | | | |
| 2002-2015 | 0 | 0 | 8 | 1^d | | | | 0 | |
| 2002-2010 | 0 | 0 | 3 | 0 | 2 | 1 | 0 | 0 | |

Table 2. SCTS breeding activity at eight preserves, 2002 - 2015, Santa Rosa Plain. Active pools are pools in which larvae were found in a given year.

^{*a*}*No larval abundance values at SCE and YUB in 2009.*

^b Introduced population and subsequent augmentation; number of active pools and larval density increasing over study period.

711 ^c Index of total number of larvae in all pools (larval density x pool volume summed for all pools in preserve).

712 ^d FEM not sampled in 2011.

^e SCTS not observed at SWP in last 5 years of the study and may have become extinct.



Figure 1. Locations of eight study preserves located on the Santa Rosa Plain: Alton (ALT),
Broadmore North (BRN), Engel (ENG), FEMA (FEM), Hall (HAL), Scenic (SCE), Southwest Park

(SWP), and Yuba (YUB). All preserves host occurring populations of SCTS except ALT, a restoredsite where SCTS were introduced.



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Figure 2. Dipnet larval abundance index (relative larval density [number of larvae captured / person-minute of sampling] x pool volume [area x ½ maximum pool depth]) and box sample larval abundance estimate at pools sampled in box sample survey (n = 13 pools, 408 1 m² box samples): y = 0.387x - 41.39; $r^2 = 0.98$, $F_{1,11} = 522.4$, p < 0.001. Excluding pool with highest values: $r^2 = 0.84$, p < 0.001, n = 12.



729

730 Figure 3. Annual SCTS larval abundance at three preserves (HAL, SWP, ENG) sampled each year by timed dipnet surveys, 2002 - 2015. Index of larval abundance = relative larval density 731 732 (number of larvae captured / person-minute of sampling) x pool volume (area x 1/2 maximum 733 pool depth). 3a: Larval abundance summed over all pools in all three preserves: $F_{1,12}$ = 8.70, p <0.02, $r^2 = 0.42$. Excluding SWP (where SCTS may have become extinct during the study): $F_{1,12} =$ 734 5.26, p < 0.05, $r^2 = 0.31$. 3b: Larval abundance for each preserve. HAL: $F_{1,12} = 7.43$, p < 0.02, $r^2 = 0.02$ 735 0.38; SWP: $F_{1,12} = 4.80$, p < 0.05, $r^2 = 0.29$; ENG: $F_{1,12} = 3.90$, p < 0.08, $r^2 = 0.24$. Pools ENG 10, 736 11, and 12 and HAL 28 were not sampled in all years and were excluded from the analysis. 737



| 739 | Figure 4. SCTS breeding activity 2002-2015 at three preserves (HAL, SWP, ENG) sampled each |
|-----|---------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| 740 | year by timed dipnet surveys 2002 - 2015. 4a: Total number of active pools (pools where larvae |
| 741 | were detected in a given year). $F_{1,12}$ = 4.91, $p < 0.05$, r^2 = 0.29. Excluding SWP: $F_{1,12}$ = 3.43, $p < 0.05$, r^2 = 0.29. Excluding SWP: $F_{1,12}$ = 3.43, $p < 0.05$, r^2 = 0.29. Excluding SWP: $F_{1,12}$ = 3.43, $p < 0.05$, r^2 = 0.29. Excluding SWP: $F_{1,12}$ = 3.43, $p < 0.05$, r^2 = 0.29. Excluding SWP: $F_{1,12}$ = 3.43, $p < 0.05$, r^2 = 0.29. Excluding SWP: $F_{1,12}$ = 3.43, $p < 0.05$, r^2 = 0.29. Excluding SWP: $F_{1,12}$ = 3.43, $p < 0.05$, r^2 = 0.29. Excluding SWP: $F_{1,12}$ = 3.43, $p < 0.05$, r^2 = 0.29. Excluding SWP: $F_{1,12}$ = 3.43, $p < 0.05$, r^2 = 0.29. Excluding SWP: $F_{1,12}$ = 3.43, $p < 0.05$, r^2 = 0.29. Excluding SWP: $F_{1,12}$ = 3.43, $p < 0.05$, r^2 = 0.29. Excluding SWP: $F_{1,12}$ = 3.43, $p < 0.05$, $r^2 = 0.05$, r |
| 742 | 0.09, r^2 = 0.22. 4b: Proportion of breeding pools active in each preserve. HAL: $F_{1,12}$ = 7.48, $p < 10^{-1}$ |
| 743 | 0.02, $r^2 = 0.38$; SWP: $F_{1,12} = 8.53$, $p < 0.02$, $r^2 = 0.42$; ENG: $F_{1,12} = 0.86$, $p > 0.30$, $r^2 = 0.07$. Larval |
| 744 | presence was not determined in all years for pools ENG 11 and 12, and HAL 28; these were |
| 745 | excluded from the analysis. |





Figure 5. Annual SCTS larval abundance and number of active pools at FEM preserve, 2002 -

2015. FEM not sampled in 2011. Larval abundance (n = 13 years): $F_{1,11}$ = 1.02, p = 0.33. Active pools (n = 13 years): $F_{1,11}$ = 5.97, p < 0.04, r^2 = 0.35.



Figure 6. Annual SCTS larval abundance and number of active pools at ALT preserve, 2002 -2015. SCTS were introduced at ALT in 1996. The population was further augmented with translocation of adults in 2004. All pools (n = 49) except one were constructed. Index of larval abundance: $F_{1,12} = 9.07$, p < 0.02, $r^2 = 0.43$. Total number of active pools: $F_{1,12} = 8.53$, p < 0.02, r^2 = 0.41.



769 Figure 7. SCTS breeding activity at 37 pools surveyed each year and hydrologic conditions,

2002-2015. Relative larval density (dipnet captures per person-minute sampled) was

significantly correlated with water availability (total precipitation – total evapotranspiration

during the SCTS breeding period [November – February]; $F_{1,12} = 6.01 r^2 = 0.330, p < 0.04$). Water

availability declined significantly over the study period ($F_{1,12} = 17.27, p < 0.001$). Precipitation

and evapotranspiration data from CIMIS Weather Observation Data for Santa Rosa, CA (Station

83a; California Department of Water Resources, 2015).

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781 Figure 8. SCTS larval density, pool depth, and predators. 8a. Mean larval density (2002 -782 2015) increased with pool depth at pools where aquatic macropredators (fish and introduced 783 crayfish) were not observed over the study period (pools without predators: $F_{1,30}$ = 8.50, p < 0.01, *n* = 32, 8); all pools *F*_{1,38} = 0.40, *p* > 0.50). Pool depths measured March 24, 2007. 8b. 784 Among pools without aquatic macropredators, deeper pools (14 year mean water depth at 785 survey) averaged greater larval density over the 2002-2015 period (Oneway ANOVA: F_{2,29}= 786 4.22, *p* < 0.03). 8c. Pools with SCTS aquatic macropredators were deeper (14 year mean) than 787 pools where these predators were not detected (*t*-test: t = 4.72, df = 38, p < 0.001). Bars 788 789 indicate standard error.