

SONOMA COUNTY CALIFORNIA TIGER SALAMANDER METAPOPULATION, PRESERVE REQUIREMENTS, AND EXOTIC PREDATOR STUDY



Contractor
Sonoma State University Academic Foundation
1801 East Cotati Avenue
Rohnert Park, California 94928

December 23, 2005

SONOMA COUNTY CALIFORNIA TIGER SALAMANDER METAPOPOPULATION, PRESERVE REQUIREMENTS, AND EXOTIC PREDATOR STUDY

Contractor

Sonoma State University Academic Foundation
1801 East Cotati Avenue
Rohnert Park, California 94928

Prepared By

David G. Cook¹

Dr. Peter C. Trenham

Dr. David Stokes

Prepared For

U. S. Fish and Wildlife Service
2800 Cottage Way, W-2605
Sacramento, California 95825-1846

FWS Agreement No.: 114203J110

December 23, 2005

¹ Mailing address: 3003 Magowan Drive, Santa Rosa, CA 95405; (707) 591-9727

TABLE OF CONTENTS

ABSTRACT.....	1
INTRODUCTION	2
Breeding and Habitat Requirements	3
Metapopulations and Conservation.....	4
METHODS	5
Study Area	5
Larval Surveys	5
Analysis.....	6
RESULTS	6
2005 Preserve Conditions	6
Pool Characteristics and Breeding Patterns	8
Natural Versus Constructed Pools	9
Preserve-Level Patterns	10
Predator Species.....	10
DISCUSSION.....	10
Status of Individual Preserves.....	11
Habitat Quality: Individual Pools and Uplands	13
Conservation at the Preserve Level: Multiple Pools.....	14
Larger Scales: The Preserve System.....	17
Additional Information Needed	17
Preserve Design	18
Management Recommendations.....	18
REFERENCES	19

APPENDIX

Tables

Table 1: Study preserve characteristics and survey dates.

Table 2: Larval capture rates at 8 study preserves, 2000-2005.

Table 3: Introduced aquatic predator species.

Figures

Figure 1: Locations of 8 study preserves located on the Santa Rosa Plain.

Figure 2: Frequency of annual activity at breeding pools compared to maximum pool depths.

Figure 3: Rainfall on the Santa Rosa Plain during Sonoma CTS breeding and larval life stages.

Figure 4: The frequency of active breeding pools at 8 study preserves from 2000 to 2005.

Figure 5: Breeding activity at constructed pools from 2001 to 2005.

Figure 6: Average maximum depths by pool type.

Figure 7: Comparison of larval capture rates and maximum depths at 54 study pools.

Figure 8: Comparison of larval capture rates at ENG and YUB pools constructed during 1999-2000 and natural pools at all preserves.

Figure 9: The number of years of breeding pool activity for 27 pools at HAL preserve from 2000 to 2005.

Figure 10: HAL preserve buffer zones around breeding pools.

ABSTRACT

This report presents results of breeding activity of the Sonoma County California Tiger Salamander (Sonoma CTS) at 8 preserves on the Santa Rosa Plain. Data collected in 2005 are combined with prior data on breeding activity at the preserves beginning in 2000 to assess critical elements of Sonoma CTS breeding ecology and conservation.

Thirty-three of the 98 study pools in the 8 preserves showed evidence of Sonoma CTS breeding activity (larvae present) in at least 1 year since 2000. Average depth of pools where Sonoma CTS larvae were found was greater than that of pools where Sonoma CTS larvae were not found. No larvae were detected in any year in pools less than 19 cm deep. The proportion of pools in which breeding occurred was lower in years with below-average winter precipitation than in years with above average winter precipitation. Breeding occurred in the smallest proportion of pools (10%) in 2002, the year of least winter rain from 2000 to 2005.

Sonoma CTS larvae were absent or low in numbers in pools with fish predators. Although crayfish are potential CTS predators, CTS larvae were present in 2 of the 3 pools in which crayfish were the only predators. Pools with potential CTS predators were significantly deeper than those without predators. These results suggest that under the conditions of the last 6 years there may be an optimum maximum pool depth of approximately 40 to 80 cm. Shallower pools may be less likely to sustain favorable conditions for CTS in dry years; deeper pools may be more likely to contain predators.

For the first time in 6 years, we found no evidence of breeding at the single pool at the Southwest Park Preserve. We also found no aquatic invertebrates and few treefrog larvae, which are normally very common, suggesting an unusual event, perhaps human-caused poisoning, occurred at the pool during the winter or spring season.

Sonoma CTS bred in constructed pools in 3 of the preserves, and additional use of constructed pools continued in 2005, with 2 pools at the Alton preserve containing CTS larvae for the first time, either a result of dispersal from the single pool where they had bred previously or the translocation of addition adults to the preserve in 2004. The 3 pools with breeding activity this year at Alton were the 3 deepest pools at the preserve. Proportions of constructed pools at Engle and Yuba preserves where CTS larvae were detected remained at their highest levels, 50% and 60% respectively. Among pools at least 19 cm deep, larvae capture rates at constructed pools did not differ significantly from capture rates at natural pools.

SONOMA COUNTY CALIFORNIA TIGER SALAMANDER METAPOPOPULATION, PRESERVE REQUIREMENTS, AND EXOTIC PREDATOR STUDY

INTRODUCTION

The Sonoma County California tiger salamander (*Ambystoma californiense*, hereafter, Sonoma CTS) forms a disjunct population that occupies the Santa Rosa Plain and adjacent lowlands of the Petaluma River watershed in Sonoma County, California. The Sonoma CTS was “emergency listed” as endangered by the U. S. Fish and Wildlife Service (USFWS) in 2002 (Wooten 2002), then downgraded to threatened status in 2004 (USFWS 2004), and then restored by court order to endangered status in 2005.

In December 2005 the USFWS approved the locally developed Santa Rosa Plain Conservation Plan instead of designating critical habitat in Sonoma County as required under the federal Endangered Species Act. This plan specifies steps necessary to establish and maintain 9 Sonoma CTS preserves totaling between 3,450 and 4,250 ac. All but 1 of our study preserves are core areas for these larger planned preserves. Also, the plan specifies monitoring and management requirements for the proposed preserves. Long-term demographic and ecological data is essential to distinguish between natural population fluctuations and actual population declines or local extinctions. Our studies of Sonoma CTS should serve as a foundation for future monitoring and initiate appropriate management actions.

Like other CTS, and amphibians generally, the Sonoma CTS is threatened by loss and degradation of habitat (Wooten 2002). The species requires vernal pools and other temporary bodies of water for breeding, and terrestrial upland habitat for growth and survival from metamorphosis to maturity and then between breeding events. Both aquatic and terrestrial habitats have been greatly reduced and degraded on the Santa Rosa Plain. As of 1994, it was estimated that vernal pool habitat on the Santa Rosa Plain had been reduced by more than 80% (Patterson et al. 1994). In addition to outright loss of habitat, the fragmented condition of the remaining habitat is likely to restrict Sonoma CTS migration between breeding and terrestrial habitats and dispersal among aquatic breeding sites.

The continued persistence of the Sonoma CTS depends on a landscape that accommodates the species' aquatic and terrestrial habitat requirements, migration and dispersal behavior, and metapopulation dynamics (Semlitsch and Bodie 1998, 2003; Trenham et al. 2000; Marsh and Trenham 2001; Semlitsch 2002). A system of preserves that maintains necessary aquatic and terrestrial habitats and allows for movement between them will be essential for recovery of the species. Currently, Sonoma CTS are known to persist in at least 10 preserves, which vary in size and include a wide range of natural and created pools. In this report we present data on the distribution of Sonoma CTS breeding activity at 8 of these preserves, and evaluate the outlook for the maintenance of viable populations.

This report builds on our previous metapopulation studies conducted at the same study sites and incorporates relevant data and analysis from 2000 to 2004 (Cook et al. 2005). This report focuses

on data collected in 2005, provides updates of the status of study preserves, and the effects of introduced predators.

Breeding and Habitat Requirements

The CTS requires both aquatic and terrestrial habitats to complete its lifecycle. For successful breeding, pools must hold water long enough for larvae to develop, but must also become dry at least periodically to eliminate fish and other aquatic predators which can prevent successful reproduction (Fisher and Shaffer 1996; Wooten 2002). Because pool permanence is positively correlated with depth, this simple measurement may be used as an indicator of breeding habitat quality. Due to our rudimentary understanding of CTS upland ecology, this habitat component is more difficult to assess, but must be extensive enough to accommodate migratory movements and must contain sufficient numbers of small mammal burrows or other underground refugia (Jennings and Hayes 1994; Petranka 1998).

Winter rainfall and pool inundation, typically occurring between November to January, trigger CTS breeding migrations (Loredo and Van Vuren 1996; Trenham et al. 2000; Cook et al. unpubl. data). Adults enter breeding pools, remain to breed for a few days or weeks, and then return to upland habitats. The eggs resulting from breeding events hatch in about 2 weeks and develop into aquatic larvae, with survivors metamorphosing and emerging from the pools as early as March or April. Emergence takes place after a minimum development period of 10 weeks (Jennings and Hayes 1994). Rain during late winter and early spring (February through April) is necessary to maintain adequate water levels, especially in shallow pools, through the aquatic larval period. Because rainfall triggers CTS breeding, inter-annual variation in the timing and magnitude of precipitation events results in highly variable yearly breeding activity and reproductive success (Trenham et al. 2000).

After leaving the breeding pond, CTS spend most of their time in small-mammal burrows. Their activities and movements at this stage are poorly known. Subadults live exclusively in upland habitats for a period of 2 to 4 years or more before breeding (Trenham et al. 2000). Most adults travel more than 100 m from their breeding pond (Trenham 2001; Trenham and Shaffer 2005). Based on radio tracking data from Monterey County, if adults are normally distributed, 95% of adults would be within 250 m of a breeding pool (Trenham 2001; Trenham *unpubl. data*). However, a more recent upland trapping study in Solano County estimated that a 630 m wide ring of habitat would be needed to encompass 95% of both adults and subadults (Trenham and Shaffer 2005). Continuing work at that site in Solano County has found that subadults are more likely to move farther from a breeding pool than adults, and they have been captured up to 1000 m from a breeding pond (Brad Shaffer, UC Davis, pers. com.). Limited information on the species' terrestrial activities suggests that while most experienced breeders return to breed at the pond where they bred previously, a substantial proportion do not. Trenham et al. (2001) found that, within a complex of 10 pools, 22% of recaptured CTS that had bred in 2 or more years were present at multiple pools. While terrestrial activities of CTS are still not well known, these indications of substantial movement suggest that to be successful, preserve design should accommodate movement between breeding pools and upland refugia and also among breeding pools.

Metapopulations and Conservation

It is widely recognized that persistence of amphibian metapopulations depends on protection of not only breeding pools and associated uplands, but the terrestrial habitat between them (Semlitsch and Bodie 1998; Trenham et al. 2000; Marsh and Trenham 2001; Semlitsch 2002). Prior to anthropogenic alteration of the Santa Rosa Plain, the area supported numerous vernal pools scattered across a landscape dominated by oak grassland vegetation, representing a large mostly continuous mosaic of suitable upland and aquatic habitat (Norwick pers. comm.). In this environment, Sonoma CTS probably functioned as a metapopulation, with sub-populations centered around vernal pools or pool complexes. Dispersal of individuals among pools resulted in genetic exchange between sub-populations, as well as rescue or recolonization of subpopulations that had declined or become extinct. Such movement is essential to the persistence of a metapopulation, allowing emigration of individuals from high quality (source) habitats to populate the diversity of habitats that comprise the full extent of the species range (Hanski and Gilpin 1991). Given the sensitivity of CTS breeding success to rainfall amounts and timing, different habitats may serve as sources in different years, buffering the metapopulation against climatic variability.

With rapid development of the Santa Rosa Plain for a variety of human uses, many vernal pools have been eliminated or degraded, and large areas of upland habitat have been converted to high intensity human uses and are unavailable for salamander use. In addition to outright loss of habitat, residential and agricultural development has also reduced terrestrial habitat quality and connectivity. Salamander populations are negatively affected by road density and terrestrial habitat alteration by humans over large scales (Houlahan and Finley 2003). In addition to causing added mortality, roads and other human landscape alterations form barriers to movement, leading to isolation of subpopulations. Isolation effects may be particularly severe where terrestrial habitats are highly fragmented or degraded (Marsh and Trenham 2001). There has been no study of the minimum number of pools needed to sustain a viable CTS metapopulation; however, it is reasonable to assume that due to climate and other sources of variability, single isolated pools may not support CTS populations with long-term viability (Trenham 2001; Trenham et al. 2000; Semlitsch and Bodie 1998). A commonly used method of mitigating for the loss or degradation of wetlands, including CTS aquatic habitat, is creation of artificial vernal pools. If these pools are suitable for CTS breeding, this could be a useful component in a strategy for enhancing the viability of and recovering the Sonoma CTS population.

In this study, we used larval surveys to characterize the extent and pattern of Sonoma CTS breeding activity over a 6-year period at 98 pools in 8 of the 10 preserves known to support the species. We standardized our pool surveys to estimate relative larval density as an indicator of breeding habitat value. We also used these data to evaluate the relative importance of preserve populations to the overall Sonoma CTS metapopulation. We also tested for differences in larval abundance and frequency of breeding activity in natural and constructed pools. Because of the critical role that timing of pool hydration and drying plays in breeding, we investigated the effect of pool depth on the value of pools as breeding habitat. We also examined the number and spatial arrangement of active breeding pools for indications of metapopulation function within preserves. Also, we evaluated the distribution of introduced aquatic predators at these preserves and the potential effects on Sonoma CTS breeding. Finally, we assessed the effectiveness of the

8 study preserves in maintaining Sonoma CTS, and developed recommendations for conservation and management of Sonoma CTS.

METHODS

Study Area

We sampled pools distributed across 8 preserves on the Santa Rosa Plain, Sonoma County, California (Figure 1). The preserves, lands protected from development for the purpose of maintaining plant and wildlife habitat, sampled were: Alton (ALT), Broadmore North (BRN), Engel (ENG), FEMA (FEM), Hall (HAL), Scenic (SCE), Southwest Park (SWP), and Yuba (YUB). All preserves had historic occurrences of Sonoma CTS, except ALT that was stocked with larvae in 1996 (C. Patterson, pers. com.) and adults in 2004 (Bill Cox, California Department of Fish and Game, pers. com.). Sampled preserves ranged in area from 1.2 ha to 69.6 ha and included 1 to 27 pools (Table 1). The physical landscape of preserves also differed with HAL, BRN, and SCE dominated by native topography, ALT, YUB, and ENG dominated by constructed pools, and SWP and FEMA containing natural but altered wetlands. Altered natural pools were probably once natural pools that were altered by excavation or impoundment. Artificial pools were designed to mimic natural vernal pools and were constructed as mitigation for the loss of natural wetlands required under section 404 of the federal Clean Water Act.

We categorized the isolation of preserves from other Sonoma CTS breeding areas based on surrounding land use and distance to additional habitat (Table 1). We determined the land use within 200 m of a preserve based on 2004 aerial photographs. Extensive urban areas (i.e., high-density residential subdivisions, large commercial complexes, and highways) were considered barriers. Rangeland, row crops, rural residential, and undeveloped land (including preserves) probably provides movement corridors and possibly terrestrial habitat, and was not considered barriers. Because CTS rarely move more than 2 km (Wooten 2002), we also considered distances of more than 2 km from the nearest known CTS observation (Rarefind 2004; DGC pers. obs.) to be a barrier. We considered preserves isolated by development or distance in all 4 cardinal directions to be highly isolated, preserves isolated in 1 to 3 directions were classified as moderately isolated, and preserves with no substantial barriers were classified as low isolation.

Larval Surveys

We conducted dip net surveys (Heyer et al. 1994) for larval Sonoma CTS during March or April (once in early May) each year from 2000 to 2005 (Table 1). During 2000, study pools at FEM, HAL, SCE, and SWP were surveyed (Table 2). YUB was added in 2001, and ALT, BRN, and ENG were included beginning in 2002. Constructed pools at ENG were built in 1999 and at YUB in 1999 and 2000. All pools with depths of at least 10 cm were surveyed. During 2005, 33 pools with depths ≤ 32 cm at ALT were not sampled so as not to disturb rare vernal pool plants with shallow pool habitat requirements. None of these pools had larvae detected during sampling from 2002 to 2004 and probably provide marginal breeding habitat due to a short hydroperiod. Pools were sampled for larvae using standard “D” shaped dip nets, swept along the pool bottom. Efforts were made to sample all aquatic habitat types in each pool (i.e., deep and shallow depths, open water, and emergent and floating vegetation). Two to 6 surveyors assisted in the survey of each pool. All surveyors were trained in the field by the same person (DGC) to ensure consistency. We timed surveys to determine capture rates. Moderate-sized pools were typically

sampled for 30 to 40 person-minutes, smaller pools were sampled with less effort and larger pools with more. In a few cases sampling was not timed and the only data recorded were larval presence or absence (Table 2). We identified all larval amphibians captured to species and released animals at the point of capture.

We estimated the maximum pool depth at all pools during 2004 by determining the elevation difference between the pool edge and the deepest point of the pool. To obtain this measurement we placed a vertical measuring pole at the deepest point in a pool and then viewed the elevation on the pole through a mounted level placed at the edge of the pool. We considered the pool edge to be at the point where vegetation changed from hydrophytic-dominated to upland-dominated plant species.

Analysis

We defined a “breeding pool” as any pool in which we detected Sonoma CTS larvae at least once during our study. An “active pool” refers to a pool in which larvae were detected during a given year. Each year we scheduled larval surveys approximately 12 weeks after breeding had occurred (Cook et al. unpubl. data; DGC pers. obs.), which corresponds to the minimum time required for eggs to hatch and larvae to develop to metamorphosis (Jennings and Hayes 1994). Pools that were dry during our survey visit could thus be determined to have been unproductive in that year.

Larval abundances were estimated as larvae captured divided by person-minute sampling. We assessed the reliability of our sampling method by resampling 5 pools at SCE during spring 2004. Surveys were on 5 and 20 March 2004 and the number of surveyors varied between 2 and 5 per sampling period. Larval capture rates did not differ significantly between surveys (Mann-Whitney $U = 1.000$, $p = 0.2222$), indicating that the method produces consistent results even when surveys are conducted on different dates by different surveyors. Descriptive and other statistics were calculated using Microsoft Excel, including mean (\bar{x}), standard deviation (s), and Student’s t -test (t), and least squares linear regression (r^2).

We obtained precipitation data from a permanent California Department of Water Resources weather station located on the Santa Rosa Plain between ALT and HAL. Average rainfall values were based on precipitation data collected since 1905 at the station.

RESULTS

The results section includes a summary of conditions at each preserve with emphasis on changes from 2004 to 2005 and updated analysis from our previous report (Cook et al. 2005) with 2005 data. The Discussion section includes the status and management recommendations for each preserve as well as the preserve system.

2005 Preserve Conditions

Alton Preserve

ALT is a wetland mitigation bank that has had a succession of vernal pool construction since probably the early 1980s. The Sonoma CTS population at ALT apparently started with the introduction of approximately 15 Sonoma CTS larvae in 1996 at pool #1 (C. Patterson pers.

com.). Larval capture rates at pool #1 have been similar during our study at 0.25 to 0.43 larvae/min. During winter 2004, 65 adults (28 females, 37 males) from west Cotati area were released into pool #1 at ALT (Bill Cox, CDFG, pers. com.). These adults did not appear to breed in spring 2004, based on similar larval abundances at pool #1. Prior to 2005 breeding was only detected in pool #1; in 2005 breeding was observed in pool #1 and 2 additional pools. The 3 pools utilized for breeding were the deepest of 43 pools sampled, ranging from 41 to 92 cm.

Broadmore North Preserve

BRN is a small mitigation preserve with 1 natural pool, but this preserve borders a larger preserve. Although the single breeding pool at this preserve is one of the shallowest studied, at 23 cm, during 4 years of sampling it has consistently produced a relatively high number of larvae (Table 2). This pool has the third highest average capture rate of larvae at 2.07 larvae/min. This preserve usually has 1 or 2 horses grazing on the site. The horses appear to limit weeds and thatch and do not appear to extensively trample or browse wetland vegetation.

Engel Preserve

ENG is a wetland mitigation bank that was recently dedicated to California Department of Fish and Game. This preserve is located in an area predominantly used as dairy rangeland and increasingly for mitigation banks. These land uses are generally conducive to Sonoma CTS. This preserve, at 16.2 ha, is much too small to be considered viable by itself. However, protection of several nearby lands, including Gobi preserve, Hale preserve, and the CDFG Todd Road preserve, increases the security of CTS locally. ENG has 11 natural and constructed pools (Table 2). Natural pool #8 has the highest larval capture rates of any pool in the study area at an average of 5.80 larvae/min and has a moderate depth of 40 cm. The reason for this relatively high productivity is not apparent, but this pool is interconnected with other pools by shallow swales that may increase water persistence later in the season and increase larval metamorphosis. Two of the constructed pools regularly contain Sonoma CTS larvae.

Pool #5 has degraded water quality conditions due to runoff from a cattle-grazing operation on an adjacent property. This pool is on the eastern border of the preserve and is part of a large swale that crosses the preserve. Pool #10 is connected to pool #5 by that swale, but has slightly better water quality. Water in pool #5 is near black in color, contains dense mats of filamentous algae, and has an odorous smell. These anoxic conditions have degraded pool quality for larvae. A few larvae were only detected in pool #5 in 1 out of 4 years of sampling (0.07 larvae/min), whereas larvae were detected in pool #10 in all 4 years (average 0.54 larvae/min).

FEMA Preserve

FEM has been severely impacted by loss of surrounding habitat and is nearly isolated by urban development (Table 1); however, the 2 altered pools at the preserve are very large and have had larvae detected during most years. Juvenile red swamp crayfish have been observed in 1 or both of the pools during 4 of the 6 years of sampling (Table 3). The source of the crayfish is likely the Roseland Channel Creek located along the north and west border of the preserve. These crayfish are omnivores and are known to prey on native amphibians, particularly eggs. This preserve borders BRN and as such the 2 should be managed as a single entity.

Hall Preserve

HAL is the largest preserve in our study, at 69.6 ha, and over 6 years we have detected larvae in 14 of the 27 pools sampled (Table 2). In 2005 we detected Sonoma CTS larvae in 7 pools. Fish were recorded at 3 pools, and fish and other predators occur in the 2 drainage channels that cross the preserve (Table 3). Pools #1 and #8 are the preserve's deepest pools at 92 cm and 54 cm, respectively. Both pools dry in the summer but are invaded by fish each winter. Larvae have never been detected in pool #1 and pool #8 has had no larvae or very low numbers annually.

Scenic Preserve

SCE is a moderately sized 9.3 ha-preserve with 5 natural pools, 4 of which have been observed to support CTS breeding (Tables 1 and 2). This preserve has natural topography but appears to have historically been used as an orchard. It is mainly grassland with a few remnant fruit trees. Recently, a conservation easement was obtained on a parcel immediately south of the preserve. Although this neighboring land has been leveled, it probably provides upland habitat for Sonoma CTS.

Southwest Park Preserve

SWP is the smallest preserve, at 1.2 ha, and paradoxically has 1 of the largest breeding pools in the study. This preserve is highly isolated and much of the surrounding land has been converted to high-density housing (Table 1). We detected Sonoma CTS larvae annually from 2000 to 2004 (Table 2). During 2005, none of the typical aquatic species were detected in our spring surveys. No Sonoma CTS larvae were detected nor were any of the typically common aquatic invertebrates. A few Pacific treefrog (*Hyla regilla*) egg masses and recently hatched tadpoles were detected, but usually this would be the most abundant species.

Yuba

YUB is a small wetland mitigation bank with 6 constructed pools. We have detected Sonoma CTS breeding in the same 3 pools in each of the past 3 years. Average larval capture rates in these pools ranged from 0.26 to 1.09 larvae/min (Table 2).

Pool Characteristics and Breeding Patterns

During our 6-year study we detected Sonoma CTS larvae at least once in 33 (33.7%) of the 98 pools sampled (Tables 1 and 2). The probability of detecting breeding activity was positively associated with pool depth. The average maximum depth of breeding pools was 42.3 cm, $s = 23.1$, $n = 33$ while non-breeding pools were significantly shallower at 24.9 cm, $s = 14.2$, $n = 65$ (t -test: $t = -3.97$, $df = 45$, $p = 0.0003$). The shallowest pool where larvae were found had a maximum depth of 19 cm deep; 77 of the 98 pools sampled were at least this deep.

Deeper pools were also generally occupied in a greater proportion of the years sampled (Figure 2; 2nd order polynomial fit: $r^2 = 0.62$, $F_{2,30} = 24.3$, $p < 0.0001$). SWP has the deepest breeding pool at 114 cm and was active each year from 2000 to 2004, but in 2005 we found no Sonoma CTS larvae, under suspicious circumstances. Pool 2 at FEM, the third deepest study pool at 93 cm, was the only pool where we detected breeding activity in all 6 years of our study (Table 2). Pool #17 at HAL was the shallowest breeding pool at 19 cm and we detected larvae only during 2004; however, this pool was dry during 3 of the 6 years of sampling.

The proportion of pools in which breeding was detected varied from year to year and appeared to be influenced by rainfall patterns (Figure 3). We observed the lowest proportions of active pools in 2000 and 2001 with 12% and 10% active, respectively. In both of these years rainfall during the winter breeding period (November through January) was below average and large fractions of the pools were already dry during our surveys. In all years with greater than average winter rainfall, pool activity rates exceeded 20%. Over the 6 years of the study yearly pool occupancy was correlated with winter rainfall ($r^2 = 0.612$). There was a weak positive correlation between spring rain and pool occupancy ($r^2 = 0.217$). We detected larvae at all preserves in almost every year, the exceptions being HAL in 2000, SCE in 2001, and SWP in 2005 (Figure 4).

Natural Versus Constructed Pools

Over the 6 years of the study, the number of constructed ponds at which Sonoma CTS breeding occurred increased at all preserves where pools have been constructed (Figure 5). In 2005 CTS larvae were found at 2 pools at ALT for the first time, in addition to the single pool where breeding has been detected each year since 2002. Proportions of constructed pools at ENG and YUB where CTS larvae were found remained at their highest levels in 2005 as well, 50% and 60% respectively.

The depths of breeding and non-breeding pools varied by pool type (Figure 6). Although constructed breeding pools were deeper on average than natural breeding pools, this difference was not statistically significant ($\bar{x}_{\text{Constructed}} = 48.6$ cm, $s = 22.8$, $n = 8$; $\bar{x}_{\text{natural}} = 34.0$ cm, $s = 13.4$, $n = 22$; t -test: $t = 1.713$, $df = 9$, $p = 0.121$). Altered breeding pools ($n = 4$) as a class had the greatest average depth. There was considerable variation in the larval capture rates for pools above the minimum depth of 19 cm and we detected no meaningful relationship between depth and capture rate (Figure 7). This suggests that there are other important factors besides depth that determine larval density.

At pools where breeding occurred, larval capture rates ranged from 0.03 to 7.39 larvae/min (Table 2). The larval capture rates in 2002 to 2005 were highly variable at both natural and constructed pools and were not statistically different ($\bar{x}_{\text{natural}} = 0.78$ larvae/min, $s = 1.34$, $n = 86$; $\bar{x}_{\text{Constructed}} = 0.75$ larvae/min, $s = 1.25$, $n = 30$; t -test: $t = -0.131$, $df = 54$, $p = 0.896$). Natural pool #8 at ENG, depth 40 cm, was the site with both the highest average larval capture rate (5.80 larvae/min) and the highest capture rate in any single year (7.39 larvae/min in 2005). The highest rate at any constructed pool was also at ENG, pool #9, during 2005 at 5.96 larvae/min (Table 2).

ENG and YUB are wetland mitigation banks with pools constructed during 1999 and 2000. Capture rates at 5 constructed breeding pools increased substantially from 2002 through 2005 (Figure 8). Sonoma CTS larvae were never detected in 6 other constructed pools at these 2 preserves (Table 2). As was the pattern for proportional pool occupancy (Figure 3), the average larval capture rates at natural breeding pools was highest in 2003 (Figure 8). Capture rates at constructed pools increased annually and were higher on average than at natural pools; however, due to extreme variability among pools within types, capture rates did not differ significantly in any of the 4 years (2002: t -test: $t = -1.087$, $df = 23$, $p = 0.288$; 2003: t -test: $t = -0.510$, $df = 23$, $p = 0.615$; 2004: t -test: $t = 0.946$, $df = 23$, $p = 0.354$; 2005: t -test: $t = 0.657$, $df = 5$, $p = 0.540$).

Preserve-Level Patterns

Preserves with fewer pools showed less year-to-year variation in number of active pools (Figure 4). Four preserves showed little or no annual variation in the numbers of active pools. BRN, FEM, and SWP contained only 1 or 2 pools. BRN and FEM contained active pools during all years of study. SWP had larvae detected in all but 1 year. ALT contained many pools >19 cm deep and larvae were observed in 3 pools in 2005. HAL and SCE each contained 5 or more pools, and showed a large variation in the pattern of pool activity. Of the 27 pools surveyed at HAL, 14 contained larvae in at least 1 year. HAL had no active pools in 2000 and a peak of 11 active pools in 2003 (Figure 4). The frequency of individual pool activity ranged from 1 to 5 years and the largest number of breeding pools were active just 2 of the 6 years sampled (Figure 9). Similarly, SCE with 5 pools varied from zero to 4 active pools annually.

Preserves varied in their isolation from other study preserves and other known Sonoma CTS breeding areas (Table 1). Surrounding land uses ranged from undeveloped to urban, and 6 of the 8 preserves were encroached upon by urban development. SWP was completely isolated by recent urbanization, while ALT was isolated by distance (>2 km) from natural Sonoma CTS populations. Moderately isolated preserves (BRN, FEM, HAL, and YUB) were encroached upon by urban development that imposed barriers to nearby Sonoma CTS areas. Preserves with low isolation (ENG and SCE) were primarily surrounded by rangeland/agricultural lands and undeveloped lands. We observed no clear relationship between preserve isolation and Sonoma CTS breeding activity or larval capture rates.

Predator Species

Potential introduced aquatic predators of Sonoma CTS embryos and larvae were found in 6 pools and 2 small channels within 3 of the preserves (Table 3). We captured native three-spine stickleback (*Gasterosteus aculeatus*), non-native mosquitofish (*Gambusia affinis*) and green sunfish (*Lepomis cyanellus*), non-native red swamp crayfish (*Procambarus clarkii*), and non-native bullfrog tadpoles (*Rana catesbeiana*). These fish species are voracious predators and presumed predators of Sonoma CTS larvae. Crayfish are known predators on amphibian eggs and may prey on CTS larvae. Bullfrogs are indiscriminant predators on native amphibians at the larval and post-metamorphic life stages. In all cases predators probably colonized naturally from adjacent perennial waterways. The crayfish found at FEM were all juveniles and were always found in pools also containing Sonoma CTS larvae. Large numbers of predators were observed in HAL pool #1 and 2 small channels that cross the preserve, and no larvae were ever detected in these habitats. HAL pool #8 contained low numbers of fish and larval capture rates in this pool were below average in all years. In 2004 no larvae were detected at HAL pool #13 where a single three-spine stickleback was detected; however, no larvae were detected here in 2003 either. In 2003 crayfish were detected in YUB pool #6 where no larvae were ever observed. Pools with predators present included some of the deepest pools in the study sample and were deeper on average than pools without predators (Pool Depths: $\bar{x}_{\text{Predators}} = 67.8 \text{ cm}$, $s = 29.4$, $n = 6$; $\bar{x}_{\text{No Predators}} = 28.2 \text{ cm}$, $s = 16.1$, $n = 92$; t -test: $t = -3.26$, $df = 5$, $p = 0.022$).

DISCUSSION

To ensure long-term persistence of Sonoma CTS, a conservation planning effort must address the salamander's habitat at a variety of spatial scales, from the individual breeding pool and

associated upland habitat, to the individual preserve, to multiple interconnected preserves and the Santa Rosa Plain as a whole. While aspects of the biology and conservation requirements of CTS remain unknown, our data and relevant findings from other studies allow several meaningful conclusions and recommendations regarding planning and management at each of these scales.

Status of Individual Preserves

Urban and agricultural encroachment and varying degrees of habitat fragmentation and isolation have affected all preserves. As discussed in below sections, existing preserves are of inadequate size and several contain too few pools. Below are specific concerns and management recommendations for individual preserves.

Alton Preserve

The primary conservation issue for ALT is the limited terrestrial habitat on and surrounding the preserve. The preserve has a limited amount of uplands due to the dense construction of artificial pools and much of the surrounding lands are urban or vineyard. Despite the limited upland habitat, ALT has maintained a small breeding population of Sonoma CTS since the initial introduction of larvae in 1996 and this population appears to be expanding. However, this may merely be due to the adult introductions in 2004. Although this expansion is encouraging, it should be noted that the removal of adults from the west Cotati area probably resulted in the extinction of that breeding population. Further, recent studies showing adaptation of populations to local habitat conditions and outbreeding depression call into question the wisdom of translocation as anything but an emergency conservation tool (Ficetola and De Bernardi 2005; Sagvik et al. 2005). The long-term potential for a sustained population of Sonoma CTS at ALT remains uncertain.

Broadmore North Preserve

BRN is adjacent to FEM and has similar habitat loss and isolation concerns by urban development. The low intensity grazing by horses appears to benefit the grasslands by reducing weeds and thatch, and cause minimal disturbance to the breeding pool. At FEM, where there is no grazing, there is a dense cover of non-native Fuller's teasel. Dense stands of vegetation may effect salamander migration, although this concern needs further study. Our confidence in the long-term potential for a sustained population of CTS at BRN would be moderate if BRN, FEM, and YUB could be made contiguous; protecting a dispersal corridor between these preserves and the CTS populations south of Ludwig Avenue would be a substantial improvement to the larger reserve.

Engel Preserve

Management concerns specific to this preserve are road mortality of migrating Sonoma CTS and questionable water quality. In fall 2005 dead adult Sonoma CTS were found along Todd Road, which borders the preserve to the south (DGC pers. obs.). Temporary road closures from November 15 to January 31 during evenings with forecasted rainfall of greater than 12 mm for a 24 hr period could greatly reduce mortality from vehicle collisions. Because no residences are located near the preserve, while inconvenient for some drivers, it is a viable option. Other options to reduce mortality would include installing tunnels below the road or elevating the road. Amphibian tunnels have been popular in Europe and they have been effective at reducing road mortality at several sites in the eastern United States. This is an option worthy of study.

Anoxic water conditions at pools #5 and #10 appear to have affected Sonoma CTS breeding and larval survival. Cattle grazing on an adjacent property appears to be the source of impairment. Although ENG has 3 highly productive pools, pool #5 is the deepest pool on the preserve. At a minimum, additional study of this apparent water quality issue is warranted. Acquiring the adjacent parcel and removing cattle would be the most effective way to improve water quality in pools #5 and #10. Cattle could also be excluded from within the watershed, an area of <1 ha, with fencing.

FEMA Preserve

Maintaining connectivity with surrounding Sonoma CTS habitats is the primary conservation concern for FEM. This preserve has become increasingly isolated by recent urban development and has been severely impacted by surrounding habitat loss. The presence of crayfish has not precluded Sonoma CTS breeding at FEM but may be affecting larval survival. The study of the effects of crayfish on egg and larvae is warranted.

Hall Preserve

Due to its relatively large size, the presence of many suitable breeding pools, and natural condition, HAL currently provides the best habitat for Sonoma CTS within any single preserve. However, most upland habitat used by Sonoma CTS breeding within HAL is probably outside the preserve. Based on Trenham and Shaffer (2005) an upland buffer of 630 m around breeding pools would be required to encompass 95% of both adults and subadults and a buffer of 380 m to encompass only 50% of salamanders. A 630 m buffer surrounding breeding pools at HAL would total 273 ha and only 25.5% of which falls within the existing preserve (Figure 10). An upland buffer containing only 50% of Sonoma CTS would require an area of 143 ha and similarly only 41.9% of this buffer is within the preserve.

The presence of fish and exotic predators at HAL is a concern. Pools #1 and #8 are deep and appear to hold water longer than any other pool on the preserve. These pools could be important sites for breeding during drought years when shallower pools dry too soon for larvae to metamorphose. A barrier fence made of fine-meshed screen could be installed between these pools and waterways to prevent fish from invading the pools. Constructing a low berm is another option, but may have negative effects on water flow patterns. The 2 channels are perennial, fed by urban runoff, but CTS do not typically breed in flowing aquatic habitats anyway.

Scenic Preserve

The size of this preserve recently increased due to the acquisition of an adjacent property that appears to include natural pools that have been filled. Pools #4 and #5 are immediately adjacent to the newly acquired land and their shoreline ends abruptly at the fence line. Restoring the native topography adjacent to these pools and increasing their size may improve water persistence and improve larval productivity. However, restoration of wetlands should be balanced with the needed for adequate upland habitat for Sonoma CTS.

Southwest Park Preserve

SWP has been severely impacted by habitat loss and isolation by urban development and only about 17.5% of the terrestrial habitat surrounding the pool remains (Cook et al. unpubl. data).

Proposed development of nearly all of the remaining uplands (James Browning, USFWS, pers. com.) will likely cause the extinction of the SWP breeding population. Also, the pool does not appear to hold water as long in the spring possibly due to hydrological changes from recent road construction and residential subdivisions.

SWP pool has been a reliable source of larvae for over a decade (Bill Cox, CDFG, pers. com.) and we detected larvae annually, except in 2005. Nearly sterile conditions in the pool were observed during the spring 2005 survey. No Sonoma CTS larvae were found and most aquatic animals that are usually found in abundance were absent, except for a few Pacific treefrog egg masses and hatchlings. We suspect that a substance was added to the pool during the winter that killed most aquatic organisms, and then after the substance had dissipated a few late-season treefrogs successfully breed at the pool. We investigated this suspicious pattern by contacting the City of Santa Rosa Parks Department and the Mosquito Abatement District. They both indicated that their staff had not visited the preserve or treated the pool. A plausible explanation is that a local resident fearing West Nile virus treated the pool with something like bleach to kill mosquito larvae. Once the bleach dissipated treefrogs returned to breed in the spring. Ironically, killing Sonoma CTS larvae would eliminate a natural effective vector biocontrol. CTS larvae are voracious predators on mosquito larvae. This event further supports the need for large buffer areas around breeding pools to reduce conflicts with urban areas.

Yuba Preserve

The long-term viability of this preserve is questionable due to its small size at 4.9 ha; however, the colonization of pools within 3 years of construction is encouraging.

Habitat Quality: Individual Pools and Uplands

Our results show that breeding pools differ substantially in depth and that this is correlated with the number of years in which Sonoma CTS larvae were detectable in a pool. The increase in breeding frequency with increased pool depth, and the complete absence of breeding in pools with a maximum depth less than 19 cm deep indicate that depth is an important determinant of pool quality. The relationship between maximum pool depth and proportion of years in which breeding occurs also suggests that populations may be buffered from climatic variability by greater pool depth.

The lack of positive effect of increased pool depth on breeding frequency beyond an intermediate depth, and the greater likelihood of predators with increasing pool depth, suggests that there may be an optimum depth for CTS pools. It appears that under the conditions of the last 6 years the optimum pool depth is approximately 40 to 80 cm. Pools shallower than the optimum may not sustain favorable conditions for CTS in all years; pools deeper than the optimum may be more likely to contain predators. However, if the prevention of predators can be assured deeper pools may be favorable.

The similar capture rates and occupancy rates of constructed and natural pools indicate that constructed pools are attractive breeding sites for Sonoma CTS. The speed with which constructed pools at ENG and YUB were colonized also indicates that newly created pools of sufficient depth are likely to be used by Sonoma CTS within a short time. The failure of Sonoma CTS to occupy more than 1 pool at ALT prior to large numbers of adult introductions in 2004

may have been a result of a small population size or the isolation from source pools. In comparison, ENG and YUB are situated near several known source pools (Rarefind 2004; DGC pers. obs.).

The rapid utilization of newly created pools suggests that additional pool creation could benefit populations in areas where breeding habitat is limited. The observation that deeper natural and constructed pools were more likely to be occupied may also be used in prioritizing areas for future protection, and in the design of additional created wetland habitat. However, because breeding habitats do not necessarily provide good upland refuges, it is essential that created breeding pools be associated with adequate upland habitats.

The positive correlation between breeding activity and pool depth highlights the potential for increasing Sonoma CTS persistence through management of habitat characteristics. This also may suggest that other methods of habitat improvement such as controlling predators, improving conditions for fossorial rodents, managing vegetation, and enhancing connectivity between occupied habitats could benefit Sonoma CTS populations.

Conservation at the Preserve Level: Multiple Pools

Metapopulation ecology provides a useful framework for management of organisms in natural and human-fragmented environments. A metapopulation is a collection of subpopulations, each semi-isolated and largely independent of the others, but with the potential for occasional exchange via dispersal. Each subpopulation has a probability of extinction such that at any given time, only some of the available habitat patches are occupied. Over time, patches shift between occupied and unoccupied status due to local extinctions and colonizations.

Because of the naturally patchy distribution of their breeding habitats, pond-breeding amphibians such as CTS have been popular subjects for metapopulation studies, and metapopulation theory has been successfully applied to conservation planning for other amphibians. The results of our study provide several observations consistent with the importance of metapopulation processes in Sonoma CTS: 1) that all suitable habitat patches are not occupied in all years; 2) deeper pools are more likely to be occupied in more years; 3) preserves with 1 or 2 pools show less variability in pool occupancy; 4) many newly constructed pools are rapidly colonized; and 5) more pools are occupied in wetter years. The shifting occupancy of pools at HAL and ENG suggests some level of metapopulation function. However, stable occupancy at sites with few pools like BRN, FEM, and SWP, along with the results of recent studies, suggest that pools within a given preserve do not support truly independent populations with high potential for extinction-colonization dynamics. Rather, based on our knowledge of CTS it seems more likely that each preserve supports a single population, perhaps with a level of spatial differentiation below that of a true metapopulation.

Due to the small size of the preserves on the Santa Rosa Plain, Sonoma CTS are capable of moving among all or most of the pools of a preserve. Thus the shifting pattern of occupancy within preserves with multiple pools would appear to be explainable by migration and the selection of different pools for breeding in different years rather than true extinctions and colonizations. Recent studies of relevance include Trenham et al. (2001), where CTS showed a 78% fidelity to breeding ponds but those 22% observed to disperse moved up to 670 m, and

Trenham and Shaffer (2005; unpublished data) where CTS were observed in upland areas up to 700 m from a central breeding pond and it was estimated that 95% of upland movements occurred within 630 m. In an experiment with pool-breeding tungura frogs (*Physataemus pustulosus*), Marsh et al. (2000) found that with shorter distances between pools males concentrate in 1 pool rather than utilizing all equally. This may explain why in ENG and HAL, where many pools are separated by a maximum distance of less than 350 m, all pools do not consistently contain larvae. The apparent lack of influence of pool isolation on occupancy at HAL also supports the single population model.

Although we expect that the 8 study preserves do not each constitute a true metapopulation, the arrangement of pools and habitats within the preserves probably exhibit some level of spatial structure and metapopulation-like dynamics, including substantial breeding site fidelity, declining Sonoma CTS numbers with greater distance from pools, and stochastic influences on small populations. These factors likely contribute to shifting occupation and “extinction” of pools and terrestrial habitat patches. To the extent that such dynamics operate, application of a metapopulation framework may be useful in preserve planning and management, and suggests that maintaining a network of pools would reduce the risk of extinction within a preserve. Even if a preserve's population has no spatial structure, there are still benefits to maintaining multiple breeding pools per preserve. Where breeding habitat is limiting, the existence of more pools increases the reproductive potential for that area. It also buffers the population against localized catastrophic events. The complete absence of Sonoma CTS larvae (and near absence of treefrog larvae and aquatic invertebrates) provides a possible example of such a catastrophic event, and suggests that the potential for such catastrophes may increase with increasing intensity of human occupation of areas near CTS preserves. Other hypothetical examples of catastrophic events are sedimentation due to nearby agricultural or construction activity or natural processes shortening pool hydroperiod to an unsuitable level.

An important question for managers is what level of redundancy of habitat patches is necessary to provide a high likelihood of population persistence. That is, how many pools and associated patches of terrestrial habitat are enough? Although it seems clear that more pools and habitat patches are more likely to ensure persistence, with limited available data and unknown future conditions it is difficult to specify a recommended number of pools.

Until we have more information about the processes determining the distribution of Sonoma CTS breeding activity, a simple and conservative approach to arriving at a crude estimate of optimal pool number is to extrapolate extinction probability at pools from the current pattern of breeding activity of all the pools that are suitable for Sonoma CTS breeding. Thus, over the course of this study, 43% of sufficiently deep pools (33 of 77 pools ≥ 19 cm deep) were found to have active breeding during any of the 6 years of the study. This suggests that at any time, 60% of suitable pools are not occupied and their populations can be assumed extinct for the purpose of this exercise. In the absence of information to the contrary, assuming independent probabilities of extinction of Sonoma CTS at each pool, a 60% extinction probability per pool would mean that each preserve should contain a minimum of 6 pools to provide a 95% likelihood of persistence, and approximately 9 pools to provide a 99% likelihood of persistence. A similar analysis, using only data from the preserve with the largest number of pools (HAL), shows that 67% (14 of 21) of sufficiently deep pools had breeding activity in any of the 5 study years. A

33% likelihood of extinction for an individual pool suggests that at least 3 pools are necessary to provide a 95% likelihood of persistence, and 4 pools to provide approximately 99% likelihood of persistence. The same analysis applied to all pools at all preserves except ALT, where an exceptionally large number of suitable pools were not active, produces results similar to the HAL analysis.

Given the approximate nature of this kind of analysis and the assumptions remaining to be investigated, this result should be considered provisional, and little significance should be attached to a specific value for pool number nor to the differences between estimates. The HAL sample may have lower extinction rates than the larger sample, but it is also a smaller sample and may not reflect some of the environmental stresses faced by Sonoma CTS at other sites. Similarly, exclusion of the ALT sample may or may not be appropriate. Furthermore, we do not yet know the extent to which metapopulation processes operate at the scale of the individual preserve. The appropriate conclusion to be drawn from this exercise is that with currently available data a first cut at the question of how many pools indicates that several--approximately 3 to 9 pools--are probably needed for a high likelihood of persistence of Sonoma CTS at a preserve. This suggests that Sonoma CTS at preserves with a very small number of pools (e.g., BRN, FEM, and SWP) may be at substantial risk of extinction.

Based on the level of breeding we found in constructed pools, and the rapidity of colonization of these pools, the provision of 3 to 9 pools per preserve is a reasonable management goal. Subsequent research on actual extinction patterns over a longer period in these multiple-pool preserves, and movement and settlement patterns of Sonoma CTS will allow refinement of probabilities and estimates of necessary pool numbers. Without very long-term studies of large numbers of populations, the true probability of extinction of subpopulations cannot be known, and even if they could be known, changing conditions due to anthropogenic (e.g. land conversion) and natural (e.g. changing weather patterns) would make projection of those probabilities into the future problematic.

Of course, pools without associated upland habitat will produce little benefit. Although each of the study preserves currently support Sonoma CTS breeding, upland habitat protection is less than optimal in all cases. Based on what we know about CTS mobility and upland habitat use, if all habitats surrounding these preserves were converted for unsuitable uses, these populations would decline in size and be more vulnerable to local extinction. Trenham and Shaffer (2005) estimate that providing less than 400 m of suitable upland habitat around pools will result in population declines of >50%. All of our study preserves provide considerably less upland habitat than this study recommends.

Because CTS commonly move hundreds of meters from breeding pools, none of the preserves are large enough to encompass the normal movements of all, or even most, salamanders emanating from the breeding pools (Trenham and Shaffer 2005). It appears that large portions of these 'preserved' populations actually occupy lands outside of the protected preserves. Even the largest preserve (HAL) contains only 25.5% of the upland habitat needed to encompass the movements of 95% of this preserve's Sonoma CTS (movement distances based on projections of Trenham and Shaffer 2005). As a result, recent and ongoing changes to land uses outside current preserve boundaries may be compromising the viability of these populations, and future

increased development of these surrounding lands can be expected to further threaten Sonoma CTS populations at the preserves. To reduce this threat, preserves must be enlarged and/or lands surrounding preserves must be managed to retain sufficient terrestrial habitat.

Larger Scales: The Preserve System

The long-term persistence probability of Sonoma CTS with the current preserve system is doubtful. Without a long-term record or any documented extinctions at whole preserves, overall extinction probabilities cannot be calculated. Clearly, however, the preserves lack the former level of large-scale connectivity that existed between patches of Sonoma CTS habitat before the large-scale anthropogenic conversion and fragmentation of the Santa Rosa Plain. The processes that probably operated to sustain the metapopulation "rescue" of populations, recolonization, infusion of genetic diversity--are characterized by low frequency and small numbers, and are therefore difficult to quantify, but they become less likely with increasing isolation of preserves. That this study did not identify isolation effects on preserve Sonoma CTS populations could be an artifact of short study period or a significant lag time in population responses to rapid landscape conversion. For example, the conversion of over half the upland habitat surrounding SWP and complete isolation has occurred in the past 6 years (Cook et al. unpubl. data), which is less than the lifespan of CTS (Jennings and Hayes 1994).

It is likely that over the long-term, isolation of preserves through ongoing habitat conversion will result in diminished metapopulation function, leading to an increased risk of extinction through well known processes of demographic and genetic stochasticity that characterize small isolated populations (Meffe and Carroll 1997). Therefore, managers should investigate opportunities to establish connectivity between preserves. Each preserve should be connected by a dispersal corridor to at least 1 other Sonoma CTS preserve, and ideally all preserves would be interconnected to form a network. These connections could be provided by dedicated preserves or by zones of unreserved lands where Sonoma CTS habitat characteristics are protected. Given that we have found that constructed pools can provide good Sonoma CTS breeding habitat, it is possible that pools can be constructed to form "stepping stones" to facilitate movement between preserves. Providing for such habitat connectivity would increase the potential for long-term persistence of the Sonoma CTS.

Additional Information Needed

To better assess extinction risk of subpopulations, as well as to track the status and trend of subpopulations and the whole population, long-term surveys are needed. The results of this study suggest that annual dip net sampling to determine the proportion of pools occupied could be an effective means for tracking the status of Sonoma CTS. Sampling must be conducted while pools still contain water, and would ideally be conducted at the same time each year. Because in many years shallower pools begin drying in early April and larvae which might have been present are then undetectable, mid- to late March is probably the optimal time for larval sampling. The most important variable to track is the proportion of pools with larval Sonoma CTS detectable by a standard level of effort per pool. The same pools should be sampled every year, including all pools on preserves that are at least 19 cm deep, or a randomly selected subset of these pools. Standardization is essential to maximizing the ability of monitoring to detect meaningful trends. Sampling pools for embryos using artificial substrates might also be considered in addition to, or in place of, dip netting for larvae (Alvarez 2004).

Another critical need for determining optimal location, size, and management of protected habitats is information on salamander movement, migration, and dispersal. This is the least known element of CTS ecology, but available evidence increasingly indicates that terrestrial habitat may limit CTS populations. Drift fence studies can be used to determine salamander densities, direction and timing of movement, spatial structuring of populations, and CTS movement corridor attributes. These kinds of studies of salamander movement are intrusive and labor intensive, so a representative sample of study locations should be identified. With a diversity of pools, relatively large extent, and diverse surrounding land uses, HAL would provide an appropriate study site. Such a study could also provide information on attributes of terrestrial habitat that influence Sonoma CTS habitat quality, including the relationship between small burrowing mammal activity and Sonoma CTS abundance.

Additional research needs include determining the pattern and timing of “colonization” of constructed pools, optimal depth of pools for CTS persistence, effects of crayfish on CTS, timing of metamorphosis of larvae and the implications for pool depth, and effects of pools size on CTS reproduction.

Preserve Design

We based our preserve model for Sonoma CTS on available ambystomid ecological, behavioral, and conservation studies. There are 3 criteria in our preserve model. First, a preserve should contain a complex of 3 or more breeding pools. We acknowledge that information on minimum pool number required to maintain a metapopulation is limited; however, single pools may not be sustainable (Trenham 2001; Trenham et al. 2000; Semlitsch and Bodie 1998). Second, maintain a terrestrial habitat buffer of 630 m surrounding breeding pools to encompass the movement and dispersal habitat of adults and juveniles (Trenham et al. 2001, Trenham and Shaffer 2005). The terrestrial buffer should contain an abundance of small burrowing mammals to provide subterranean refugia for salamanders. Third, the minimum preserve size should be approximately 200 ha to maintain a viable population. We based this preserve size on a hypothetical pool complex where three 30-m-radius pools are distributed linearly, this would require a preserve at least 1.75 km by 1.29 km, totaling 190 ha. In practice, the geometry of pools and surrounding uplands should influence the shape of preserves.

None of the 8 study preserves met all of the preserve criteria. The multiple breeding pool criterion was met at 5 preserves, although FEM only contained 2 breeding pools. The terrestrial buffer and size criteria were not met at any of the preserves and all preserves are too small. The ability of Sonoma CTS to move distances >630 m suggest that large portions of Sonoma CTS populations occupy upland habitats beyond preserve boundaries.

Management Recommendations

Based on our data and the findings of other studies, we offer the following conservation and management recommendations:

1. Preserves should include at least 3 pools, and 4 to 9 pools would be preferable. Preserves with few pools should have additional pools constructed. It is reasonable to expect that some of these constructed pools will be occupied by Sonoma CTS.

2. All pools relied upon to support Sonoma CTS breeding should be 40 to 80 cm or deeper and isolated from fish-bearing bodies of water. To ensure sufficient volume, each pool should have surface areas on the order of 0.1 ha or more.
3. Substantial upland habitat, at least 630 m, from each pool should be included in preserves. Where such preserve boundaries are too small to encompass habitat at that distance, land use should be regulated to protect Sonoma CTS habitat, habitat features (e.g. fossorial rodents), and connectivity to suitable uplands.
4. At least 3 of the pools within a preserve should be at least 200 m apart to promote some degree of independence.
5. Linkages (connecting movement corridors) between preserves should be maintained where they currently exist.
6. Where linkages between preserves do not exist, they should be connected through habitat preservation or promoting maintenance of habitat features in non-preserve lands. Constructed pools may provide stepping-stone habitats facilitating dispersal between distant preserves. Existing barriers in movement corridors should be altered to permit Sonoma CTS passage.
7. Research should be conducted on several critical unknowns. These include: patterns of terrestrial movement and settlement of Sonoma CTS adults and juveniles, potential for upland habitat enhancement, effects of exotic predators, and continued monitoring of Sonoma CTS breeding activity to better characterize patterns of colonization, occupancy, and extinction of pools.

REFERENCES

- Alvarez, J. A. 2004. Use of an artificial egg laying substrate to detect California tiger salamanders (*Ambystoma californiense*). *Herpetological Review* 35: 45-46.
- Cook, D. G., D. Stokes, P. C. Trenham, and P. T. Northen. 2005. Metapopulation dynamics and preserve requirements for the California tiger salamander in Sonoma County. Sacramento: U. S. Fish and Wildlife Service, Sacramento Field Office. 29 p.
- Ficetola, G. F., and F. de Bernardi. 2005. Supplementation or *in situ* conservation? Evidence of local adaptation in the Italian agile frog *Rana latastei* and consequences for the management of population. *Animal Conservation* 8:33-40.
- Fisher R. N., H. B. Shaffer. 1996. The decline of amphibians in California's Great Central Valley. *Conservation Biology* 10:1387-1397.
- Hanski, I., and M.E. Gilpin. 1991. *Metapopulation dynamics*. Academic Press, London.
- Heyer, W. R., M. A. Donnelly, R. W. McDiarmid, L. C. Hayek, and M. S. Foster, editors. 1994. *Measuring and Monitoring Biological Diversity, Standard Methods for Amphibians*. Smithsonian Institution Press, Washington, D.C.
- Houlahan, J. E., and C. S. Findley. 2003. The effects of adjacent land use on wetland amphibian species richness and community composition. *Canadian Journal of Fisheries and Aquatic Sciences* 60:1078-1094.
- Jennings, M. R., and M. P. Hayes. 1994. *Amphibian and reptile species of special concern in California*. Rancho Cordova: California Department of Fish and Game, Inland Fisheries Division.
- Loredo, I. and D. van Vuren. 1996. Reproductive ecology of a population of the California tiger salamander. *Copeia* 1996:895-901.

- Marsh, D. M., Rand, A. S., and Ryan, M. J. 2000. Effects of inter-pond distance on the breeding ecology of tungara frogs. *Oecologia* 122: 503-513.
- Marsh, D. M. and P. C. Trenham. 2001. Metapopulation dynamics and amphibian conservation. *Conservation Biology* 15:40-49.
- Meffe, G. K., and C. R. Carroll. 1997. *Principles of Conservation Biology* 2nd Ed. Sinauer Associates. Sunderland MA.
- Patterson, C. A., Guggolz, B., and M. Waaland. 1994. Seasonal wetland baseline report for the Santa Rosa Plain, Sonoma County. California Dept. of Fish and Game.
- Petranka, J. W. 1998. *Salamanders of the United States and Canada*. Smithsonian Institution Press, Washington, D.C. 587p.
- Rarefind 2004. California Natural Diversity Data Base maintained by California Department of Fish and Game, Sacramento, CA.
- Sagvik, J., T. Uller and, M. Olsson. 2005. Outbreeding depression in the common frog, *Rana temporaria*. *Conservation Genetics* 6:205-211.
- Semlitsch, R. D., and J.R. Bodie. 1998. Are small, isolated wetlands expendable? *Conservation Biology*. 12:1129-1133.
- Semlitsch, R. D. 2002. Critical elements for biologically based recovery plans of aquatic-breeding amphibians. *Conservation Biology* 16:619-629.
- Semlitsch, R. D. and J. R. Bodie. 2003. Biological criteria for buffer zones around wetlands and riparian habitats for amphibians and reptiles. *Conservation Biology* 17:1219-1228.
- Trenham, P. C., H. B. Shaffer, W. D. Koenig, and M. R. Stromberg. 2000. Life history demographic variation in the California tiger salamander (*Ambystoma californiense*). *Copeia* 2000: 365-377.
- Trenham, P. C. 2001. Terrestrial habitat use by adult California tiger salamanders. *Journal of Herpetology* 35:343-346.
- Trenham, P. C., W. D. Koenig, and H. B. Shaffer. 2001. Spatially autocorrelated demography and interpond dispersal in the salamander *Ambystoma californiense*. *Ecology* 82:3519-3530.
- Trenham, P.C, and H.B. Shaffer. 2005. Amphibian upland habitat use and its consequences for population viability. *Ecological Applications* 15:1158-1168.
- U. S. Fish and Wildlife Service (USFWS). 2004. Endangered and threatened wildlife and plants; determination of threatened status for the California tiger salamander, and special rule exemption for existing routine ranching practices. *Fed Reg.* 69:47211-47248.
- Wooten, D. E. (USFWS) 2002. Endangered and threatened wildlife and plants; listing the Sonoma County distinct population segment of the California tiger salamander as endangered. *Fed. Reg.* 67:47726 - 47740.

APPENDIX

Tables

Table 1: Study preserve characteristics and survey dates.

Table 2: Larval capture rates at 8 study preserves, 2000-2005.

Table 3: Introduced aquatic predator species.

Figures

Figure 1: Locations of 8 study preserves located on the Santa Rosa Plain.

Figure 2: Frequency of annual activity at breeding pools compared to maximum pool depths.

Figure 3: Rainfall on the Santa Rosa Plain during Sonoma CTS breeding and larval life stages.

Figure 4: The frequency of active breeding pools at 8 study preserves from 2000 to 2005.

Figure 5: Breeding activity at constructed pools from 2001 to 2005.

Figure 6: Average maximum depths by pool type.

Figure 7: Comparison of larval capture rates and maximum depths at 54 study pools.

Figure 8: Comparison of larval capture rates at ENG and YUB pools constructed during 1999-2000 and natural pools at all preserves.

Figure 9: The number of years of breeding pool activity for 27 pools at HAL preserve from 2000 to 2005.

Figure 10: HAL preserve buffer zones around breeding pools.

Table 1: Study preserve characteristics and survey dates. For each preserve we provide the total area of the preserve, and the number of constructed, altered natural, and natural pools sampled. Numbers in parentheses represent the number of pools of each type where we detected Sonoma CTS larvae at least once during the study. Surrounding land uses included undeveloped (U), rangeland/agricultural (RA), residential rural (RR), and urban (UR). We based isolation on physical barriers from UR and distances > 2 km separating preserves from other breeding pool areas. Double dash indicates no survey conducted, na = not applicable, nd = no data.

Characteristic	Preserve								Total
	ALT	BRN	ENG	FEM	HAL	SCE	SWP	YUB	
Preserve Area (ha)	18.2	5.3	16.2	32.0	69.6	9.3	1.2	4.9	156.6
Pool Type									
Constructed	43(3)	0	5(2)	0	0	0	0	6(3)	54
Altered	0	0	0	2(2)	0	0	1(1)	1	4
Natural	1	1(1)	6(3)	0	27(14)	5(4)	0	0	40
Total	44	1	11	2	27	5	1	7	98
Construction	pre1988-99	na	1999	nd	na	na	nd	1999-00	
Surrounding Land Use									
North	R/RA	U	RA	UR	RR/UR	RR/UR	UR/U	RR	
East	RR	RR	RA	UR/RR	UR	UR/RR	UR/U	RR	
South	RA/RR	RR	U/RA	U/RR	UR	RA	UR	RR	
West	RA	U/UR	U/RA	UR/U	RA	RR/RA	UR	U/UR	
Isolation Category	High	Mod.	Low	Mod.	Mod.	Low	High	Mod.	
Larval Survey Dates									
2000	--	10-Apr	--	10-Apr	7-Apr	7-Apr	31-Mar	--	
2001	--	22-Apr	--	22-Apr	22-Apr	17-Apr	19-Mar	3-May	
2002	15-Mar	28-Mar	28-Mar	28-Mar	17-Mar	25-Mar	1-Mar	28-Mar	
2003	7-Mar	7-Mar	6-Mar	7-Mar	8-Mar	6-Mar	6-Mar	7-Mar	
2004	13-Mar	19-Mar	19-Mar	19-Mar	20-Mar	20-Mar	13-Mar	19-Mar	
2005	20-Mar	11-Mar	18-Mar	11-Mar	25-Mar	18-Mar	11-Mar	18-Mar	

Table 2: Larval capture rates at 8 study preserves, 2000-2005. Data from breeding pools shown are of timed larval sampling at preserves on the Santa Rosa Plain. Pools with estimated maximum depths > 19 cm are shown. Preserve codes are defined in the Methods section. Pools at ALT < 32 cm were not sampled during 2005 to avoid disturbance to rare plants. Three types of pools were sampled: natural (N), altered natural (A), and constructed (C). Larval capture rates were estimated as the number of larvae captured per minute of sampling. Not all preserves were surveyed during 2000 and 2001. An “*” indicates that larvae were detected but capture rate could not be calculated Double dash indicates no survey conducted and "Dry" indicates a pool was completely dry at the time of our survey.

Preserve	Pool ID	Pool Type	Depth (cm)	Larval Capture Rate By Year						AVG
				2000	2001	2002	2003	2004	2005	
ALT	1	C	70	--	--	0.26	0.43	0.35	0.25	0.32
	2	C	92	--	--	0.00	0.00	0.00	0.18	0.04
	3	C	34	--	--	0.00	0.00	0.00	0.00	0.00
	4	C	32	--	--	0.00	0.00	0.00	0.00	0.00
	6	C	30	--	--	0.00	Dry	0.00	0.00	0.00
	7	C	23	--	--	0.00	Dry	0.00	0.00	0.00
	8	C	29	--	--	0.00	0.00	0.00	--	0.00
	9	C	27	--	--	0.00	Dry	0.00	--	0.00
	11	C	27	--	--	0.00	0.00	0.00	--	0.00
	13	C	35	--	--	0.00	0.00	0.00	0.00	0.00
	14	C	19	--	--	0.00	Dry	Dry	--	0.00
	15	C	21	--	--	0.00	Dry	0.00	--	0.00
	16	C	41	--	--	0.00	0.00	0.00	0.86	0.22
	17	C	30	--	--	Dry	Dry	0.00	0.00	0.00
	18	C	22	--	--	Dry	0.00	0.00	--	0.00
	19	C	23	--	--	Dry	0.00	0.00	--	0.00
	21	C	23	--	--	Dry	Dry	Dry	--	0.00
	22	C	24	--	--	Dry	0.00	0.00	--	0.00
	23	C	23	--	--	Dry	0.00	0.00	--	0.00
	25	C	19	--	--	Dry	Dry	0.00	--	0.00
	26	C	20	--	--	Dry	Dry	0.00	--	0.00
	27	C	33	--	--	Dry	0.00	0.00	0.00	0.00
	28	C	29	--	--	Dry	Dry	Dry	--	0.00
	29	C	22	--	--	Dry	0.00	0.00	--	0.00
	30	N	25	--	--	Dry	0.00	0.00	--	0.00
	30a	C	19	--	--	Dry	Dry	0.00	--	0.00
	32	C	29	--	--	Dry	0.00	0.00	--	0.00
	33	C	29	--	--	Dry	0.00	0.00	--	0.00
	34	C	20	--	--	Dry	Dry	0.00	--	0.00
	36	C	24	--	--	Dry	Dry	0.00	--	0.00

	39	C	21	--	--	Dry	0.00	0.00	--	0.00
	40	C	25	--	--	Dry	0.00	0.00	--	0.00
	41	C	29	--	--	Dry	0.00	0.00	--	0.00
BRN	3	N	23	--	--	1.40	1.80	3.44	1.65	2.07
ENG	3	C	23	--	--	0.00	0.00	1.00	0.06	0.27
	4	C	21	--	--	0.00	0.00	0.00	0.00	0.00
	5	N	47	--	--	0.00	0.00	0.07	0.00	0.02
	7	N	28	--	--	Dry	Dry	Dry	0.00	0.00
	8	N	40	--	--	6.80	3.63	5.38	7.39	5.80
	9	C	26	--	--	*	2.70	1.87	5.96	3.51
	10	N	34	--	--	*	0.19	0.83	0.59	0.54
	11	C	26	--	--	0.00	0.00	0.00	0.00	0.00
FEM	1	A	54	0.12	0.03	0.17	0.78	1.00	0.79	0.48
	2	A	93	0.00	0.03	0.04	0.06	0.31	0.20	0.11
HAL	1	N	97	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	2	N	41	Dry	Dry	0.14	0.31	0.00	0.04	0.08
	3	N	39	0.00	Dry	0.00	0.00	0.00	0.00	0.00
	4	N	20	Dry	Dry	Dry	0.00	Dry	0.00	0.00
	5	N	34	Dry	0.08	0.44	1.57	1.06	2.50	0.94
	6	N	31	Dry	Dry	0.10	0.00	0.00	0.00	0.02
	7	N	23	Dry	Dry	0.00	0.00	0.00	0.00	0.00
	8	N	54	0.00	Dry	0.00	0.03	0.15	0.27	0.08
	9	N	24	Dry	Dry	0.00	1.13	0.00	0.57	0.28
	10	N	23	Dry	Dry	0.21	0.00	Dry	0.00	0.03
	11	N	32	Dry	Dry	0.73	1.78	0.00	0.00	0.42
	12	N	27	Dry	Dry	1.80	1.50	0.00	0.00	0.55
	13	N	22	Dry	Dry	0.65	1.88	0.00	0.00	0.42
	14	N	25	Dry	Dry	0.00	0.00	0.00	0.00	0.00
	15	N	30	Dry	Dry	1.00	1.00	0.94	0.45	0.57
	16	N	28	Dry	Dry	0.00	0.00	0.00	0.00	0.00
	17	N	19	Dry	Dry	Dry	0.00	0.42	0.00	0.07
	19	N	37	0.00	Dry	0.33	0.40	0.00	0.22	0.16
	25	N	23	Dry	Dry	Dry	0.25	0.00	0.00	0.04
	26	N	20	Dry	Dry	Dry	0.14	0.00	0.76	0.15
	27	N	23	Dry	Dry	Dry	0.00	Dry	0.00	0.00
SCE	1	N	75	*	0.00	0.82	0.60	0.50	1.47	0.68
	2	N	41	0.00	Dry	0.00	Dry	Dry	0.00	0.00
	3	N	49	*	Dry	1.56	0.30	0.48	0.22	0.51
	4	N	36	0.00	Dry	0.40	0.96	0.00	0.71	0.34
	5	N	26	0.00	Dry	1.33	1.67	0.21	0.00	0.54
SWP	1	A	114	*	1.15	5.29	0.10	2.28	0.00	1.76

YUB	1	C	46	--	0.00	0.00	1.60	2.83	1.04	1.09
	2	C	44	--	0.00	0.00	0.00	0.00	0.00	0.00
	3	C	51	--	0.00	0.00	0.71	0.60	0.36	0.33
	4	C	40	--	0.00	0.10	0.29	0.67	0.26	0.26
	5	C	37	--	Dry	0.00	0.00	0.00	0.00	0.00
	6	A	87	--	Dry	0.00	0.00	0.00	0.00	0.00
				AVG	0.00	0.04	0.31	0.34	0.32	0.50

Table 3: Introduced aquatic predator species. Preserves and pools with observed predators are listed. Species observed included red swamp crayfish (C), three-spine stickleback (S), mosquitofish (M), green sunfish (G), and bullfrog tadpole (B). Double dash indicates no survey conducted.

Preserve	Pool ID	CTS Breeding	Year					Comment	
			2000	2001	2002	2003	2004		2005
FEM	1	Yes		C			C		Near Roseland Creek
	2	Yes				C	C	C	Near Roseland Creek
HAL	1	No	S	S	T, M	S	S, M	S	Connected to ditch
	8	Yes			S	C	S, G	C	Adjacent to small ditch
	13	Yes					S		Adjacent to pond
	North Channel	No	C, S, M, B		--	--	--	S	Perennial ditch, urban runoff
YUB	South Channel	No	C, T, M, B		--	--	--	C, S	Perennial ditch, urban runoff
	6	No				C			Pool is altered ditch

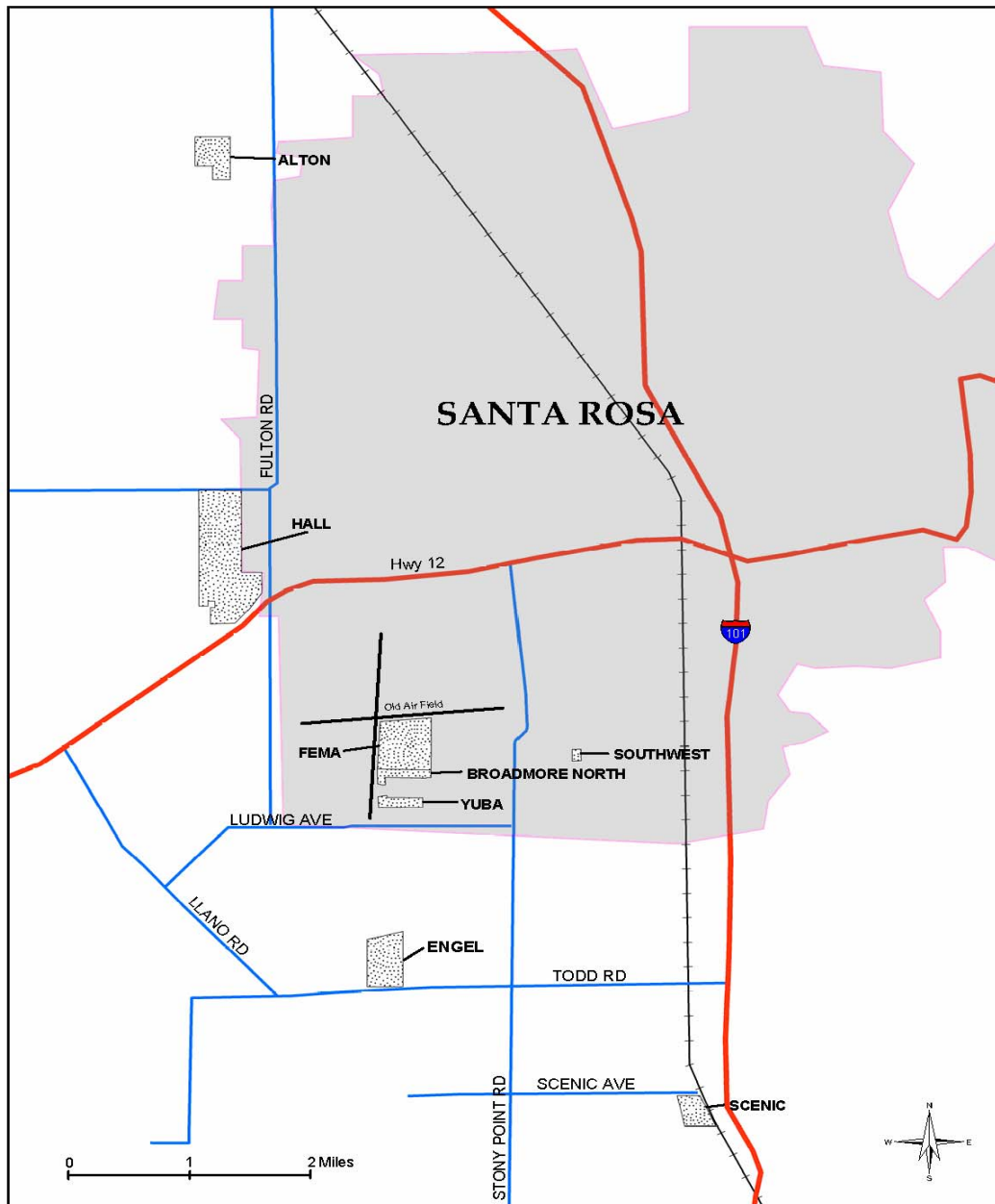


Figure 1: Locations of 8 study preserves located on the Santa Rosa Plain.

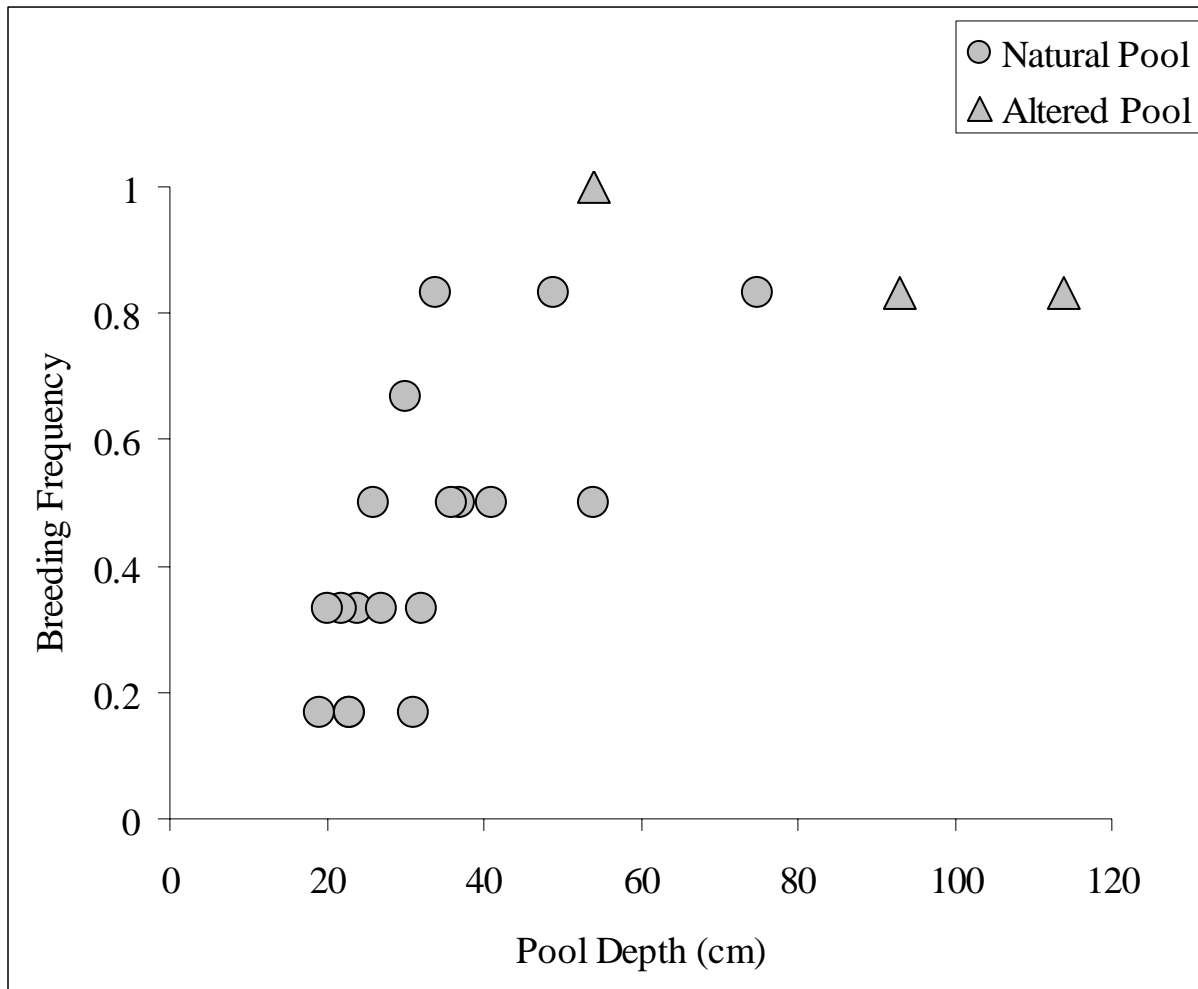


Figure 2: Frequency of annual activity at breeding pools compared to maximum pool depths. Breeding pools (n = 21) are shown from FEM, SWP, HAL, and SCE that were sampled annually from 2000 to 2005.

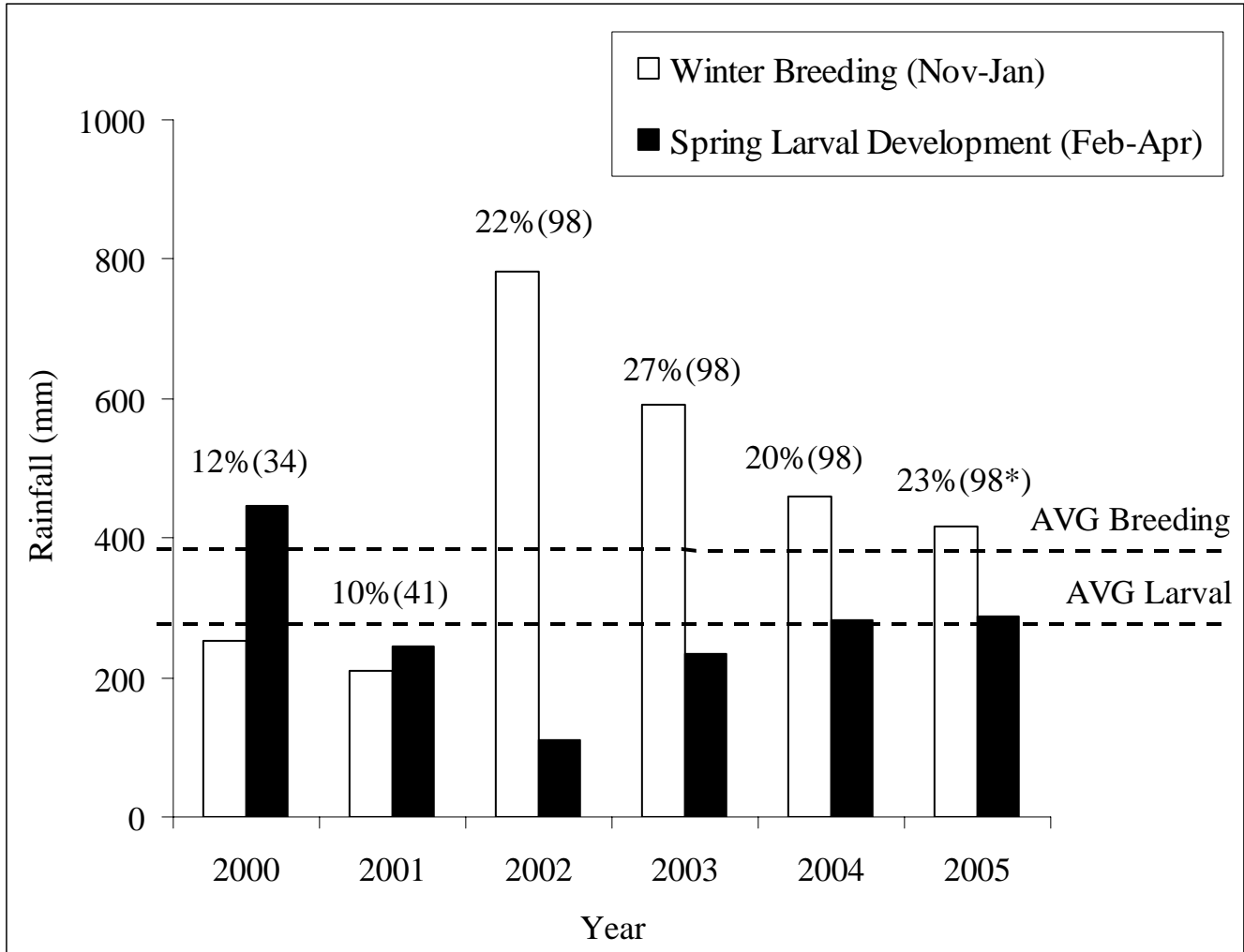


Figure 3: Rainfall on the Santa Rosa Plain during Sonoma CTS breeding and larval life stages. Percentages are active pools and numbers in parentheses indicate total pools sampled. * During 2005 at ALT 33 of 44 pools were not sampled that had shallow depths and marginal breeding habitat, and the shown percent active pools is based on 98 study pools. See Table 2 for preserves and pools sampled by year.

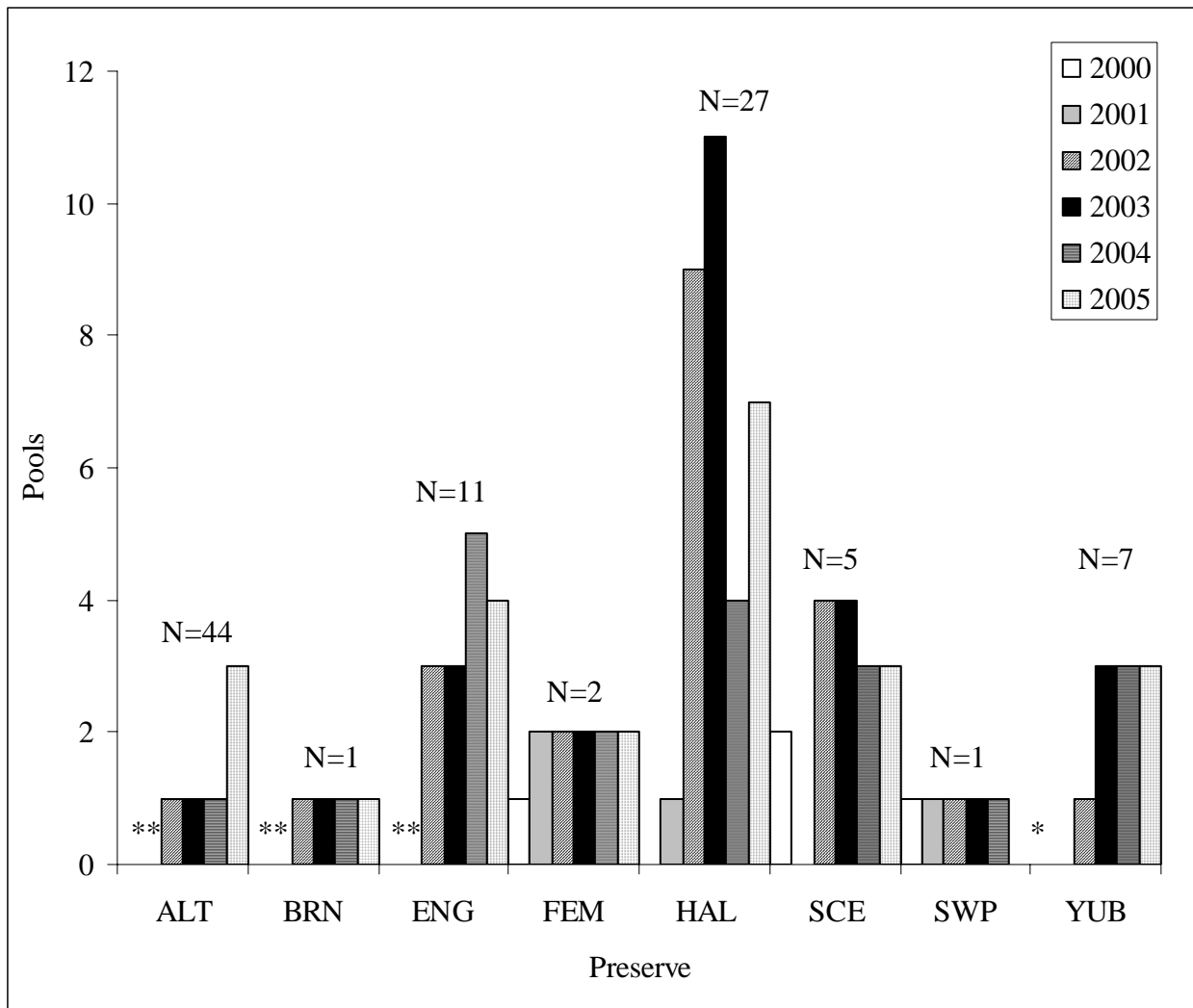


Figure 4: The frequency of active breeding pools at 8 study preserves from 2000 to 2005. N values are number of sampled pools per year. Asterisk indicates no data for a survey year.

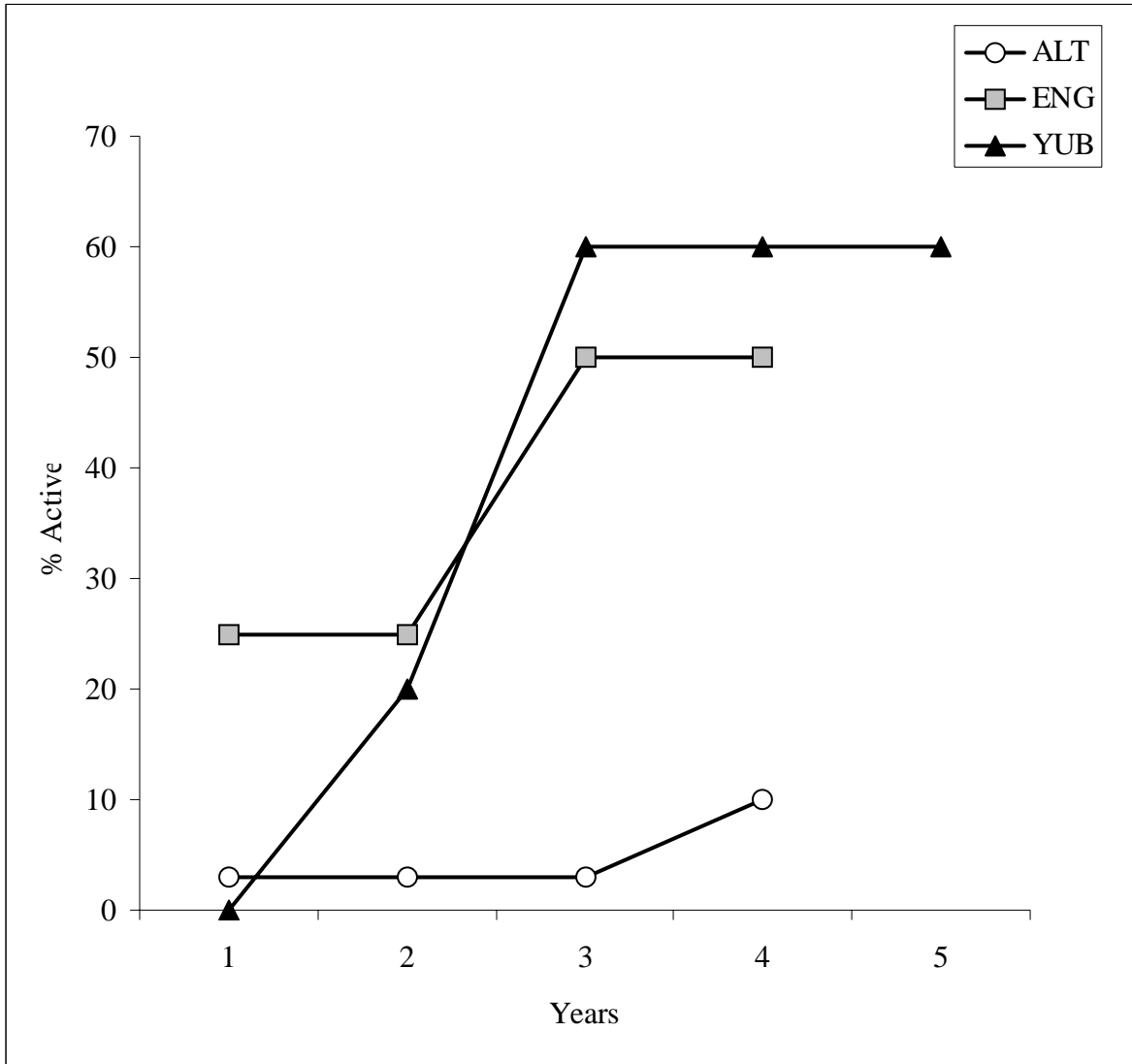


Figure 5: Breeding activity at constructed pools from 2001 to 2005. The number of constructed pools of adequate depth (≥ 19 cm) in which larvae were detected has increased at all preserves with constructed pools (ALT, ENG, YUB). X-axis indicates years since surveys were begun.

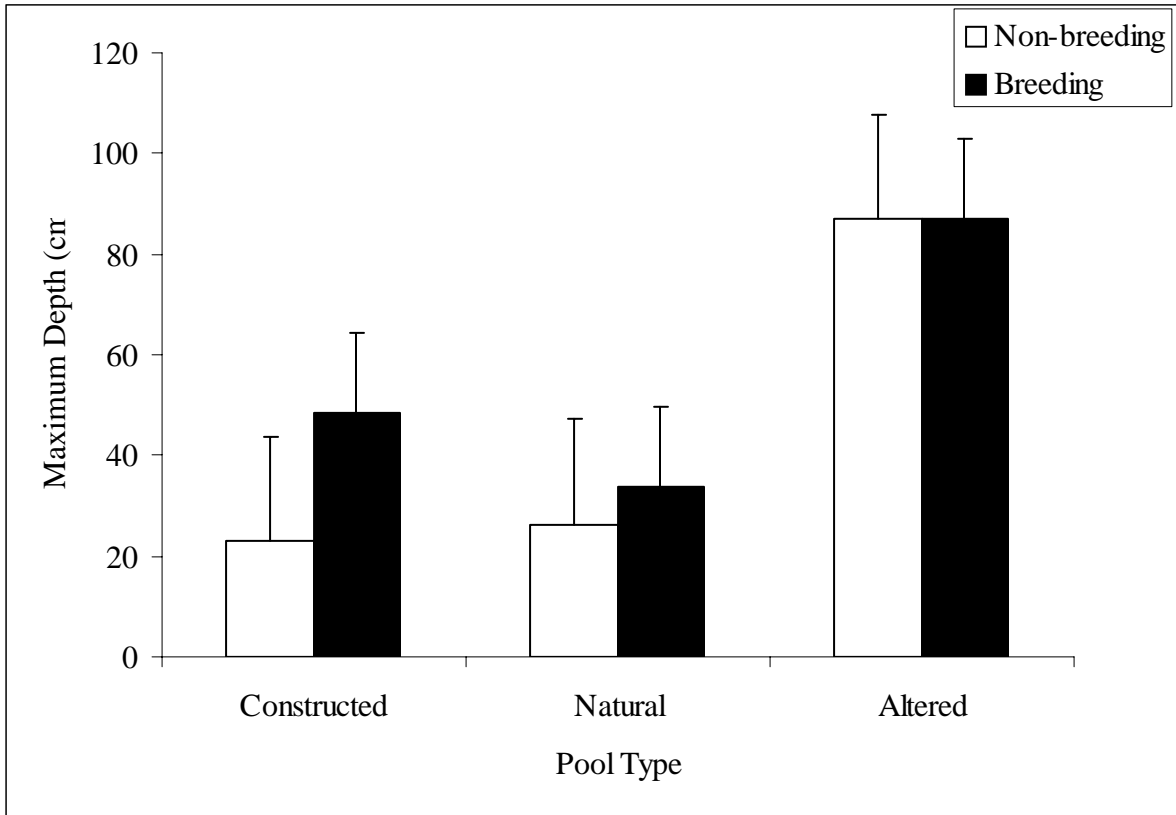


Figure 6: Average maximum depths by pool type. Sample pools included 54 constructed, 40 natural, and 4 altered pools. Whiskers indicate standard error values.

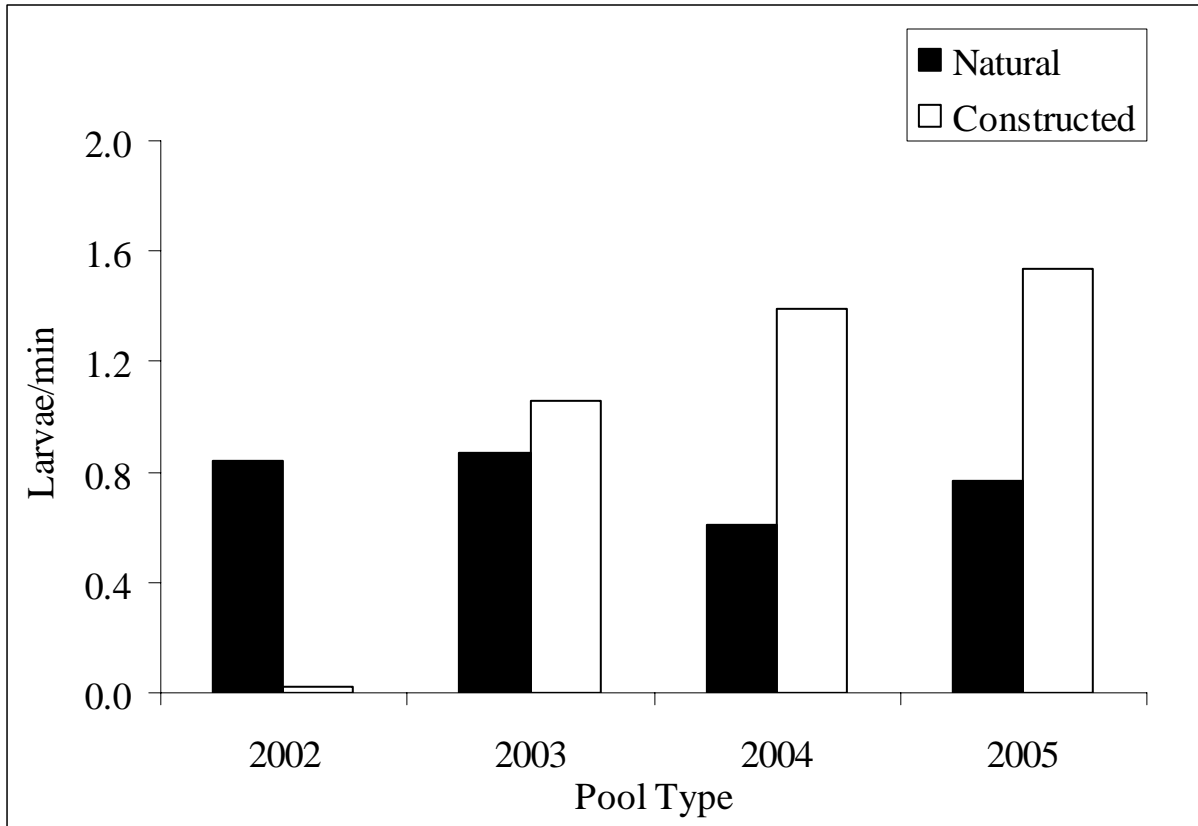


Figure 8: Comparison of larval capture rates at ENG and YUB pools constructed during 1999-2000 and natural pools at all preserves. Sample size by pool type were 22 natural and 5 constructed. ENG pools 9 and 10 were excluded from 2002 due to incomplete data.

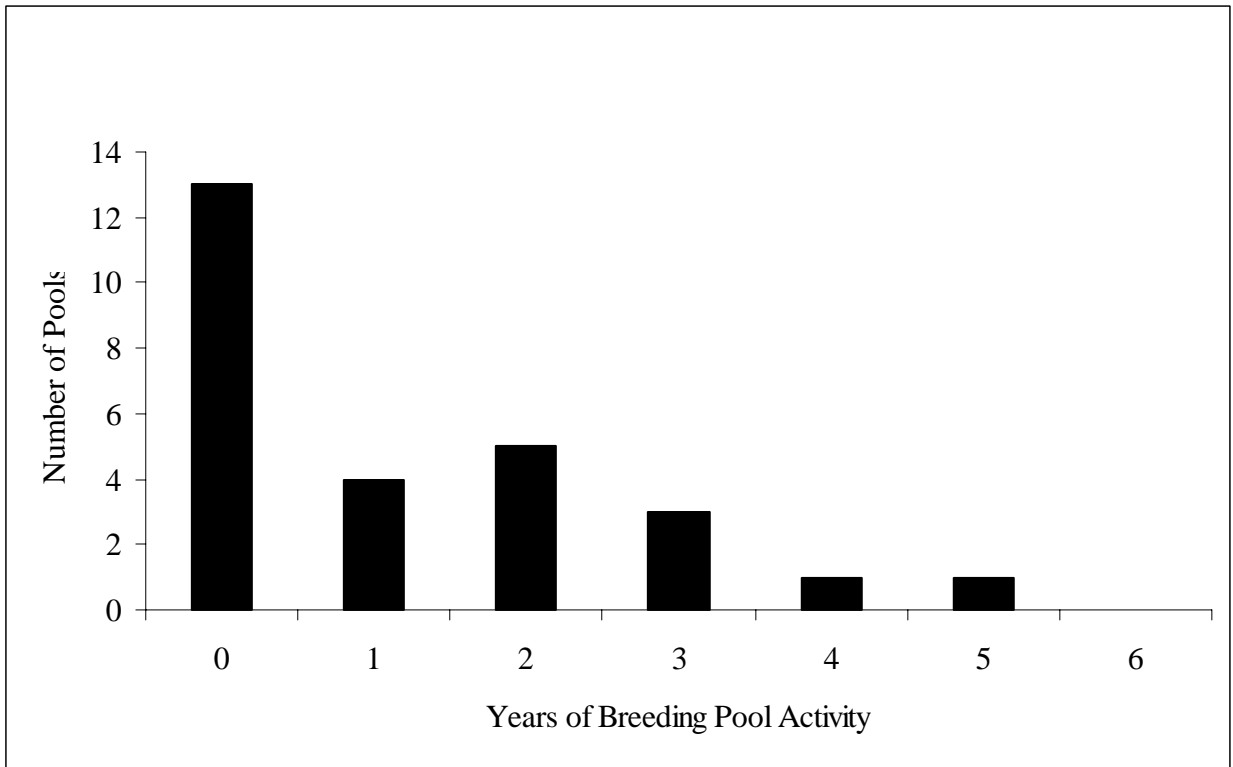


Figure 9: The number of years of breeding pool activity for 27 pools at HAL preserve from 2000 to 2005. Thirteen pools were never occupied and no pools were active during all 5 years of study.



Figure 10: HAL preserve buffer zones around breeding pools. Active breeding indicates larvae detected at least once from 2000 to 2004. An upland buffer of 630 m is required to encompass 95% of both adults and subadults and a buffer of 380 m to encompass 50% of salamanders.