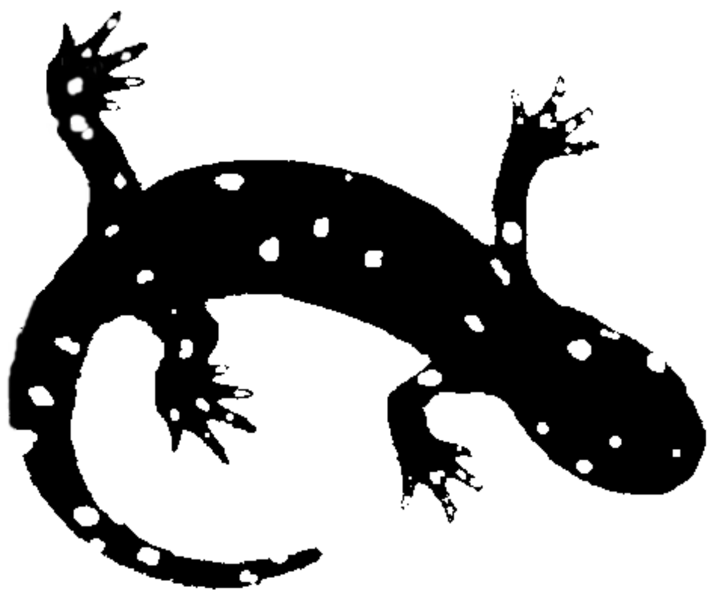
WORKSHOP

BIOLOGY AND MANAGEMENT OF THE CALIFORNIA TIGER SALAMANDER (*Ambystoma californiense*)



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Timeline of Events in the History of *Ambystoma californiense*

1853 Species named by John Edward Gray (Keeper of Zoology at the British Museum)

1925 Tracy Storer publishes the first detailed description of the species and its habits

1971 CDFG suggests CTS be added to list of protected amphibians

1982 CDFG adds CTS to Special Animal List (later Species of Special Concern)

1985 USFWS places CTS in Category 2 list of candidate species for ESA listing

1992 USFWS considers proposal for listing CTS under ESA

1994 USFWS concludes that listing is "warranted but precluded" by higher priorities

2000 USFWS lists Santa Barbara County distinct population segment as endangered

2003 USFWS lists Sonoma County distinct population segment as endangered

2004 USFWS lists Central distinct population segment as threatened

- listing includes 4d rule exempting routine ranching procedures from regulation

2010 CDFG lists CTS as threatened throughout their range

Glossary of Terminology Used

Adult – A tiger salamander that is capable of breeding. Breeding adult males are identifiable by their swollen vent and enhanced tail fin. Sex can be difficult to assign accurately outside of the breeding season. Most adults are >80 mm SVL.

Aestivation – A sleep-like state of complete inactivity and reduced metabolism like hibernation, but occurring during the summer. Although tiger salamander aestivation is commonly discussed, no author has ever published a report of aestivating California tiger salamanders. Upland habitat is sometimes called aestivation habitat.

Fossorial – Adapted for digging. Tiger salamanders do not dig their own burrows, but rather occupy the burrows of fossorial mammals.

Egg – An unfertilized ovum.

Embryo – The stage from egg fertilization through emergence from the embryonic jelly coat. Inseminated females attach embryos to grass and other debris in shallow portions of breeding ponds.

Juvenile – The stage of development between metamorphosis and adulthood. These look like adults in coloration and morphology, but are usually smaller.

Larva – The aquatic free-swimming gilled stage of development beginning after emergence from the embryonic jelly coat and ending at metamorphosis.

Metamorph – The brief and transient period of development between aquatic larval development and the completely terrestrial juvenile stage. Metamorphs are intermediate in morphology and coloration, often with partially resorbed gills and tail fins and a little of the final color pattern observable. Metamorphs are usually detected in and around breeding ponds in spring and summer.

Metamorphosis – The process of transformation from an aquatic larva to a terrestrial juvenile. During this process gills and tail fins are resorbed and coloration and the overall morphology begins to change to the terrestrial form. Larvae beginning metamorphosis can be detected by inspection of their gills and tail fin.

Paedomorph – In permanent ponds, larvae of *A. mavortium* sometimes become sexually mature larvae, living a completely aquatic life and never metamorphosing. This phenomenon has never been observed in *A. californiense*, but may occur in hybrids.

Spermatophore – A sperm capped cone of jelly that male salamanders deposit on the ground or pond-bottom and female salamanders pick up with their cloacae facilitating internal fertilization.

Subadult – A term essentially meaning the same thing as juvenile, above.

Annotated Bibliography of the Main CTS References (updated 4/2023)

- Alvarez, J.A. 2004. Overwintering California tiger salamander (*Ambystoma californiense*) larvae. Herpetological Review 35:344.

Although *A. mavortium* larvae commonly remain larval for >1 year in permanent water habitats, this was the first observation of *A. californiense* remaining larval into their second winter. However, *A. californiense* are still not thought to form sexually mature larvae (paedomorphs)

- Alvarez, J.A. 2004. Use of artificial egg laying substrate to detect California tiger salamanders (Ambystoma californiense). Herpetological Review 35:45-46.

CTS embryos were found in many pools where later in the season no larvae were detected. Explains method for creating laying substrates to non-destructively sample for embryos.

- Anderson, J.D. 1968. A comparison of the food habits of Ambystoma macrodactylum sigillatum, *Ambystoma macrodactylum croceum*, and *Ambystoma tigrinum californiense*. Herpetologica 24:273-284.

Young *A. californiense* larvae eat primarily small zooplankton with larger individuals shifting to a diet focused largely on tadpoles of *Pseudacris regilla* and *Rana draytonii.*

- Austin, C.C. and H.B. Shaffer 1992. Short, medium, and long-term repeatability of locomotor performance in the tiger salamander, *Ambystoma californiens*e. Functional Ecology 6:145-153.

Endurance, but not burst speed, of individual CTS changes over the course of 15 months.

- Bain, T. K., D. G. Cook, and D. J. Girman. 2017. Evaluating the effects of abiotic and biotic factors on movement through wildlife crossing tunnels during migration of the California tiger salamander, *Ambystoma californiense*. Herpetological Conservation and Biology 12: 192-201.

CTS are more likely to successfully use wildlife tunnels when there is greater precipitation. Moisture within the tunnel itself increases the speed with which CTS move through the tunnel, but not their probably of successfully crossing.

- Barry, S.J. and H.B. Shaffer. 1994. The status of the California tiger salamander (*Ambystoma californiense*) at Lagunita: a 50-year update. Journal of Herpetology 28:159-164.

Summary of the ecology, natural history and history of the CTS population on Stanford's campus. Established strategy still used for managing the draw-down of Lagunita to minimize larval CTS mortality.

- Brehme, C.S., J.A. Tracey, B.A.I. Ewing, M.T. Hobbs, A.E. Launer, T.A. Matsuda, E.M. Cole Adelsheim and R.N. Fisher. 2021. Responses of migratory amphibians to barrier fencing inform the spacing of road underpasses: a case study with California tiger salamanders (Ambystoma californiense) in Stanford, CA, USA. Global Ecology and Conservation 31:e01857.

CTS only move an average of 40 m along fencing before turning back. It is thus recommended that there should be short (<12.5 m) distances between road crossing structures. This would allow >90% of CTS to pass successfully. Barrier fencing should also be solid rather than mesh.

- Cook, D.G., P.C. Trenham and P.T. Northen. 2006. Demography and breeding phenology of the California tiger salamander (*Ambystoma californiense*) in an urban landscape. Northwestern Naturalist 87:215-224.

Drift fence study of breeding migrations at a large vernal pool in an urbanizing area of Santa Rosa, Sonoma County. Adults were captured as they arrived at the breeding pond in 1999, 2002 and 2003. Total numbers of adults estimated to be breeding at this pond ranged from 65 to 107. Whereas some males arrived at the ponds following the first rains, females only arrived in substantial numbers after the pond filled. Yearly breeding migrations began anywhere from November to January, depending on rainfall.

- Cook, D.G., L.R. Stemle, D.L. Stokes, A.F. Messerman, J.A. Meisler and C.A. Searcy. 2023. Habitat value of constructed breeding pools for the endangered Sonoma population of California tiger salamander. Journal of Wildlife Management 87:e22370.

Density of larval CTS is positively associated with both pond depth and pond area. Once correcting for these factors, CTS densities in constructed ponds are equal to those in natural ponds.

- Cooper, R.D. and H.B. Shaffer. 2021. Allele-specific expression and gene regulation help explain transgressive thermal tolerance in non-native hybrids of the endangered California tiger salamander (Ambystoma californiense). Molecular Ecology 30:987-1004.

Hybrids between California tiger salamanders and barred tiger salamanders have higher thermal maximums than either parental species. They also exhibit greater variance in thermal maximums than either parental species. Mean thermal maximum in all three groups is approximately 34°C.

- Davidson, C., H.B. Shaffer and M.R. Jennings. 2002. Spatial tests of the pesticide drift, habitat destruction, UV-B, and climate-change hypotheses for California amphibian declines. Conservation Biology 16:1588-1601.

Whereas upwind pesticide use is strongly correlated with the disappearance of four of California's ranid frogs, no similar correlation was observed for CTS disappearance sites. For CTS the most significant difference between extant and extirpated sites was that extant sites had significantly less urbanized land within 5km.

- Fisher, R.N. and H.B. Shaffer. 1996. The decline of amphibians in California's Great Central Valley. Conservation Biology 10:1387-1397.

Documented rarity of native amphibians in the low elevation portions of the Central Valley. Attributed decline to habitat loss and disturbance in the agricultural Central Valley and also introduced predators. First peer reviewed study of general decline in California.

- Fitzpatrick, B.J. and H.B. Shaffer. 2004. Environment dependent admixture dynamics in a tiger salamander hybrid zone. Evolution 58:1282–1293.

In an area where *A. mavoritum* were introduced by bait dealers, hybrids of *A. mavoritum* and *A. californiense* are now present. Genetic assays indicated that salamanders present in permanent constructed ponds contained greater proportions of *A. mavoritum* alleles; ephemeral constructed ponds and natural vernal pools generally contained more *A. californiense* alleles. Eliminating permanent ponds by draining or physical modification may limit the spread of hybrid genes.

- Fitzpatrick, B.M. and H.B. Shaffer. 2007. Introduction history and habitat variation explain the landscape genetics of hybrid tiger salamanders. Ecological Applications 17:598-608.

The current distribution of introduced alleles is largely contained in the Salinas Valley. The spatial transition from highly mixed genetic makeup to nearly pure native populations was abrupt, suggesting either cryptic barriers to dispersal or locally rapid displacement of natives by an advancing hybrid swarm. At a more ecological level, highly modified perennial breeding ponds had higher introduced allele frequencies than more natural seasonal ponds, suggesting greater invasion success in perennial breeding ponds.

- Fitzpatrick, B.M. and H.B. Shaffer. 2007. Hybrid vigor between native and introduced salamanders raises new challenges for conservation. Proceedings of the National Academy of Sciences of the United States of America 104:15793-15798.

Genetic analysis suggests that larvae containing an intermediate mixture of genes from native and introduced tiger salamanders have higher survivorship than those containing mostly native or mostly introduced genes. Suggests that hybrids might spread.

- Fitzpatrick, B.M., J.R. Johnson, D.K. Kump, J.J. Smith, S.R. Voss and H.B. Shaffer. 2010. Rapid spread of invasive genes into a threatened native species. Proceedings of the National Academy of Sciences of the United States of America 107:3606-3610.

Genetic assessments of samples along a transect from Salinas to Alameda County indicate that in general genes from the introduced tiger salamanders have not spread far beyond the sites of original introduction. <u>However</u>, three genes show a very different pattern with rapid spread far beyond the apparent sites of introduction, indicating that natural selection is favoring the spread of these markers. This complicates the assessment of hybrid versus native status. An example from Fort Ord shows that only one population has a large fraction of introduced genes for markers other than these exceptional markers – for the exceptional markers all populations are fixed for two of these non-native markers.

- Holland, D.C., M.P. Hayes and E. McMillan. 1990. Late summer movement and mass mortality in the California tiger salamander (AMBYSTOMA CALIFORNIENSE). Southwestern Naturalist 35:217-220.

An unusual August rainstorm initiated a mass migration of recently metamorphosed salamanders from a large pond in San Luis Obispo County. Large numbers of these animals died on the surface and under debris.

- Holland, R.F. 1998. Great Valley vernal pool distribution, photorevised. Pages 71-75 in C.W. Witham et al., editors. Ecology, conservation, and management of vernal pool ecosystems. California Native Plant Society, Sacramento.

Using air photos, estimated the area of vernal pool complexes remaining and also the areas lost since an earlier study. Estimates are on a county-wide basis and cover only the Central Valley. (http://www.dfg.ca.gov/whdab/wetlands/vp_holland/report_index.htm)

- Jennings, M.R. 1996. *Ambystoma californiense*. Burrowing Ability. Herpetological Review 27:194.

Description of an *A. californiense* digging its way through a burrow plug to enter a pocket gopher burrow. Use of these burrows was known but this was the first observation of a salamander forcing its way into a plugged burrow.

- Johnson, J.R., B.B. Johnson and H.B. Shaffer. 2010. Genotype and temperature affect locomotor performance in a tiger salamander hybrid swarm. Functional Ecology 24:1073-1080.

Migration rate increases with ambient temperature. For hybrids between *A. californiense* and *A. mavortium*, F1 hybrids have the greatest movement capacity.

- Johnson, J.R., B.M. Fitzpatrick and H.B. Shaffer. 2010. Retention of low-fitness genotypes over six decades of admixture between native and introduced tiger salamanders. BMC Evolutionary Biology 10:147.

For hybrids between *A. californiense* and *A. mavoritum*, non-native backcrosses have the highest survival, while F2s have the lowest. Size at metamorphosis is an additive trait, time at metamorphosis shows dominance, and survival exhibits epistasis. There are still many low-fitness hybrid genotypes present in the wild after 60 years of natural selection.

- Johnson, J.R., R.C. Thomson, S.J. Micheletti and H.B. Shaffer. 2011. The origin of tiger salamander (*Ambystoma tigrinum*) populations in California, Oregon, and Nevada: introductions or relicts? Conservation Genetics 12:355-370.

Introduced populations of *A. mavoritum* exist in northern and southern California and in the Sierra Nevada. Populations of tiger salamanders near the Oregon border are potentially native *A. mavortium* as they are most closely releated to Washington populations.

- Johnson, J.R., M.E. Ryan, S.J. Micheletti, and H.B. Shaffer. 2013. Short pond hydroperiod decreases fitness of non-native hybrid salamanders in California. Animal Conservation 16:556-565.

Documents a fitness advantage of native California tiger salamanders relative to hybrids and barred tiger salamanders in rapidly drying mesocosms.

- Joseph, M.B., D.L. Preston, and P.T.J. Johnson. 2016. Integrating occupancy models and structural equation models to understand species occurrence. Ecology 97:765-775.

Demonstrates the negative effect of non-native fish on presence of CTS.

- Loredo, I., D. Van Vuren and M.L. Morrison. 1996. Habitat use and migration of the California tiger salamander. Journal of Herpetology 30:282-285.

Following the initial night of emigration by adult and recently metamorphosed CTS at a Contra Costa County site, they found that 83% of adults disappeared into ground squirrel holes while 54% of new metamorphs entered ground squirrel holes and 46% surface cracks. Occupied and unoccupied ground squirrel burrows were used equally. Adults moved up to 129 m and new metamorphs up to 57 m.

- Loredo, I. and D. Van Vuren. 1996. Reproductive ecology of a population of the California tiger salamander. Copeia 1996:895-901.

Three year study of one breeding pond in Contra Costa County. Metamorph production was 1248, 481 and 3 across these three seasons. Some new metamorphs marked in the first year of the study were later recaptured as 2 year old breeding adults. The timing of breeding migrations was strongly correlated with rainfall events.

- Marty, J.T. 2005. Effects of cattle grazing on diversity in ephemeral wetlands. Conservation Biology 19:1626-1632.

Grazing increases cover of native species and decreases cover of introduced species. It also increases the species richness of both plants and aquatic invertebrates and increases hydroperiod.

- McDevitt-Galles, T., W.E. Moss, D.M. Calhoun, C.J. Brigss and P.T.J. Johnson. 2022. How extreme drought events, introduced species, and disease interact to influence threatened amphibian populations. Freshwater Science 41:680-694.

CTS respond strongly to drought conditions, both in terms of absence from breeding sites during drought and rapid recovery following drought. During the 2013-2016 drought, CTS disappeared from 87% of breeding sites. Presence and density of CTS is also negatively associated with invasive fish and American Bullfrogs.

- Messerman, A.F., A.G. Clause, S.V.L. Catania, H.B. Shaffer and C.A. Searcy. 2021. Coexistence within an endangered predator-prey community in California vernal pools. Freshwater Biology 66:1296-1310.

Documents prey of all CTS life stages. Larval CTS have a clear preference for the largest prey that will fit inside their mouths – anuran tadpoles or tadpole shrimp, depending on geographic location. Larvae and, to a lesser extent, breeding adults have much larger gut contents than strictly terrestrial life stages due to the abundance of prey in the breeding ponds.

- Messerman, A.F., A.G. Clause, L.N. Gray, M. Krkosek, H.B. Rollins, P.C. Trenham, H.B. Shaffer and C.A. Searcy. 2023. Applying stochastic and Bayesian integral projection modeling to amphibian population viability analysis. Ecological Applications 33:e2783.

Despite CTS populations being able to withstand high levels of human-induced mortality, it is estimated that a ~1000 m buffer of terrestrial habitat is needed to maintain population viability. Growth of terrestrial CTS is projected to have the strongest influence on population growth rate.

- Moss, W.E., T. McDevitt-Galles, E. Muths, S. Bobzien, J. Purificato and P.T.J. Johnson. 2021. Resilience of native amphibian communities following catastrophic drought: Evidence from a decade of regional-scale monitoring. Biological Conservation 263:109352.

In drought conditions, probability of CTS presence increases in permanent ponds and decreases in temporary ponds. Similar to many other California amphibians, CTS recovery quickly post-drought. Colonization probability of CTS decreases with presence of fish and proportion of developed land.

- Orloff, S.G. 2011. Movement patterns and migration distances in an upland population of California tiger salamander (*Ambystoma californiense*). Herpetological Cosnervation and Biology 6:266-276.

Five year effort to capture and remove CTS from a large development project in Contra Costa County revealed a large number of adult and subadult CTS on the order of 1000 m from known breeding ponds. Animals did not appear to use any obvious corridors in the landscape and were roughly evenly distributed. Even after fiver years of drift fence trapping, significant numbers of salamanders remained within the proposed project area.

- Padgett-Flohr, G.E. and J.E. Longcore. 2005. *Ambystoma californiense*. Fungal infection. Herpetological Review 36:50-51.

Evidence of “chytrid” fungal infection in wild-caught Santa Clara County CTS larvae.

- Petranka, J.W. 1998. Salamanders of the United States and Canada. Smithsonian Institution Press, Washington DC, pp. 47-50.

Good summary of literature available in 1998, but misses many later publications.

- Picco, A.M., J.L. Brunner and J.P. Collins. 2007. Susceptibility of the endangered California tiger salamander, *Ambystoma californiense*, to Ranavirus infection. Journal of Wildlife Diseases 43:286-290.

Infection has not been documented in the field, but susceptibility is documented, emphasizing the importance of minimizing potential for introduction of this agent.

- Polich, R.L., C.A. Searcy and H.B. Shaffer. 2013. Effects of tail-clipping on survivorship and growth of larval salamanders. Journal of Wildlife Management 77:1420-1425.

Recommends larval tail-clipping as a method for collecting genetic samples. In a mesocosm study, there was no detectable effect of tail-clipping on either growth or survival of larval CTS, even when up to 20% of the larvae's total length was removed.

- Pyke, C. 2005. Assessing suitability for conservation action: prioritizing interpond linkages for the California tiger salamander. Conservation Biology 19:492-503.

Used complex models to assess habitat connectivity of known breeding ponds in Santa Barbara County, and to prioritize areas for conservation action. Model shows three to five remaining subareas which are fairly well connected by intact upland habitat corridors.

- Pyke, C. and J. Marty. 2005. Cattle grazing mediates climate change impacts on ephemeral wetlands. Conservation Biology 19:1619-1625

Grazing played an important role in maintaining the suitability of vernal pool hydrological conditions for fairy shrimp and salamander reproduction. Without grazing, after 3 years pools dried an average of 50 days earlier.

- Riley, S.P.D., H.B. Shaffer, S.R. Voss and B.M. Fitzpatrick. 2003. Hybridization between a rare, native tiger salamander (*Ambystoma californiense*) and its introduced congener. Ecological Applications 13:1263–1275.

First published evidence of hybridization between native *A. californiense* and introduced *A. mavortium.* Populations studied were in the Salinas Valley, Monterey County.

- Ryan, M.E., J.R. Johnson and B.M. Fitzpatrick. 2009. Invasive hybrid tiger salamander genotypes impact native amphibians. Proceedings of the National Academy of Sciences 106:11166-11171.

In artificial ponds, hybrids reduce the growth and survival of native California tiger salamanders. In ponds with hybrids, far fewer newts and treefrogs survived to metamorphosis. This study indicates that hybrids not only displace native CTS but adversely affect them where the two co-occur and strongly impact other species.

- Ryan, M.E., J.R. Johnson, B.M. Fitzpatrick, L.J. Lowenstine, A.M. Picco and H.B. Shaffer. 2012. Lethal effects of pond water quality on threatened California salamanders but not on co-occurring hybrid salamanders. Conservation Biology 27:95-102.

Dramatic die-offs of California tiger salamander larvae were observed in late spring (April/May) in experimental enclosures in Salinas Valley ponds. A veterinary pathologist involved with the project determined that larvae were starving and oxygen-stressed, likely due to chemical exposure. Data did not suggest disease or pathogens as the cause. Ponds experiencing die-offs had approximately 10x more pesticide applications within 1.6 km in the weeks leading up to these observations that occurred in the area around ponds without die-offs.

- Searcy, C.A. and H.B. Shaffer. 2008. Calculating biologically accurate mitigation credits: insights from the California tiger salamander. Conservation Biology 22:997-1005.

The authors used upland capture rates in traps 10, 100, 200, 300, 400, 500, 600, 700, 850 and 1000 m from Olcott Lake (a large playa pool) in Solano County. Adult and juvenile CTS were captured at all distances, but numbers captured declined with distance from the pond. On average, approximately 1 adult and 7 juveniles per trap were captured 1 km out from the pond, while at 100 m averages per trap were 27 juveniles and 10 adults. These results indicate that lots of CTS are hundreds of meters from the pond. The authors suggest a method for assigning mitigation value based on salamander densities.

- Searcy, C.A. and H.B. Shaffer. 2011. Determining the migration distance of a vagile vernal pool specialist: How much land is required for conservation of California tiger salamanders? Pages 73-87 in D.G. Alexander and R.A. Schlising (Eds.), Research and Recovery in Vernal Pool Landscapes. Studies from the Herbarium, Number 16. California State University, Chico, CA.

Uses 15,212 capture events to estimate that 95% of CTS are within 1867 m of their breeding pond, which is similar to the USFWS determination that all land within 2092 m of a breeding pond is CTS habitat. This suggests that CTS could serve as an umbrella species for 89 other listed species that share this habitat.

- Searcy, C.A., E. Gabbai-Saldate and H.B. Shaffer. 2013. Microhabitat use and migration distance of an endangered grassland amphibian. Biological Conservation 158:80-87.

Demonstrates that adult CTS tend to occupy areas with flood intolerant vegetation and juvenile CTS tend to occupy higher elevation microhabitats. CTS have the second longest median migration distance (556 m) recorded among salamanders.

- Searcy, C.A., L.N. Gray, P.C. Trenham and H.B. Shaffer. 2014. Delayed life history effects, multi-level selection, and evolutionary tradeoffs in the California tiger salamander. Ecology 95:68-77.

Shows that mean cohort fitness of metamorph CTS varies by more than one order of magnitude and is related to mean body mass of the individuals in the cohort. Also documents an evolutionary tradeoff in which selection over the first summer of terrestrial life favors earlier metamorphosis, while all subsequent selection favors a larger body size. This tradeoff could help maintain the large variation in mean cohort mass/fitness.

- Searcy C.A. and H.B. Shaffer. 2014. Field validation supports novel niche modeling strategies in a cryptic amphibian. Ecography 37:983-992

This paper includes important information regarding the habitat features that make localities suitable or unsuitable for CTS presence.

- Searcy, C.A., H. Snaas, and H.B. Shaffer, 2015. Determinants of size at metamorphosis in an endangered amphibian and their projected effects on population stability. Oikos 124:724-731.

Uses a combination of experimental and field data to examine the environmental factors determining both number of successfully metamorphosing CTS larvae and individual size at metamorphosis. Demonstrates that density of CTS larvae is the most important factor determining size at metamorphosis, thus creating a negative feedback loop that will stabilize population fluctuations. Also demonstrates that prey availability and pond hydroperiod have positive impacts on both number and size of CTS metamorphs, emphasizing the importance of these variables in CTS life history.

- Searcy, C.A., H.B. Rollins, and H.B. Shaffer. 2016. Ecological equivalency as a tool for endangered species management. Ecological Applications 26:94-103.

Uses mesocosm experiments to investigate the community-level effects of different CTS/hybrid genotypes. Concludes that superinvasives (5% non-native genes) fulfill the same ecological role as pure CTS and thus should be protected under the Endangered Species Act. Concludes that full hybrids (70% non-native genes) fulfill some of the ecological role provided by pure CTS, but depress their prey to lower densities, which could be a conservation concern in settings where those prey are also endangered. Also suggests decreasing pond hydroperiods as a management technique for making natural selection favor a higher frequency of native CTS genes.

- Searcy, C.A. and H.B. Shaffer, 2016. Do ecological niche models accurately identify climatic determinants of species ranges? The American Naturalist, 187:423-435.

Combines ecological niche modeling and field data to demonstrate that the same climatic factors setting the range limits for CTS also determine inter-annual fluctuations in local population sizes. The most important climate factors are 1) annual precipitation, 2) mean minimum temperature of the coldest month, and 3) mean diurnal range. Study then uses this model to predict which regions of California will be most suitable for CTS under predicted climate change scenarios.

- Shaffer, H.B., C.C. Austin and R.B. Huey. 1991. The consequences of metamorphosis on salamander (*Ambystoma*) locomotor performance. Physiological Zoology 64:212–231.

In the lab they found that salamanders on a treadmill can walk at 5 cm/s for about 8 minutes (20 m) before succumbing to exhaustion. *more recent studies have shown this to be temperature dependent – at higher temperatures they can walk farther.

- Shaffer, H.B., J.M. Clark and F. Kraus. 1991. When molecules and morphology clash: a phylogenetic analysis of the North American ambystomatid salamanders (Caudata: Ambystomatidae). Systematic Zoology 40:284-303.

Early evolutionary analysis of the tiger salamanders of North America in which the authors try to resolve conflicting results of protein and morphological variation.

- Shaffer, H.B., R.N. Fisher and S.E. Stanley. 1993. Status report: the California tiger salamander (*Ambystoma californiense*). Final report to the California Department of Fish and Game.

Summary of state-wide surveys of known historic localities and also available suitable habitat. In many cases they were unable to find CTS at historic sites, sometimes because no habitat to sample remained. These data went into the later paper by Fisher and Shaffer (1996). Contains data on habitat, water quality and predators at most sampled sites.

- Shaffer H.B and M.L. McKnight. 1996. The polytypic species revisited: genetic differentiation and molecular phylogenetics of the tiger salamander *Ambystoma tigrinum* (Amphibia: Caudata) complex. *Evolution* 50:417–433.

Based on mitochondrial DNA variation, they find *A. californiense* to be a strongly differentiated and unique group, but the rest of the picture is less clear. All other species in this group are more closely related to each other than they are to *A. californiense*. CTS were isolated 5 million years ago.

- Shaffer, H.B., G.B. Pauly, J.C. Oliver and P.C. Trenham. 2004. The molecular phylogenetics of endangerment: cryptic variation and historical phylogeography of the California tiger salamander, *Ambystoma californiense.* Molecular Ecology 13: 3033-3049.

Identified 6 genetic groups of CTS in different parts of California. Sonoma and Santa Barbara County groups were the most distinct, possibly even warranting recognition as separate species. Other distinct, but less deeply diverged, groups were centered around the San Francisco Bay Area, the Central Valley, the Central Coast region, and the Southern San Joaquin Valley. Results suggest it may be important to avoid mixing CTS from different areas (i.e., from salvage efforts).

- Shaffer, H.B. and P.C. Trenham. 2005. The California tiger salamander (*Ambystoma californiense*). In M.J. Lannoo (Ed.), Status and Conservation of U.S. Amphibians. University of California Press, Berkeley, CA.

Complete overview of CTS status, ecology, and natural history.

- Stokes, D.L., A.F. Messerman, D.G. Cook, L.R.Stemle, J.A. Meisler and C.A. Searcy. 2021. Saving all the pieces: an inadequate conservation strategy for an endangered amphibian in an urbanizing area. Biological Conservation 262: 109320.

Documents trends in the endangered Sonoma County DPS from 2002-2020. CTS larval densities have decreased by 48% over this period. Preserves with multiple ponds and at least one pond capable of supporting metamorphosis even in dry years are those with less negative population trends.

- Storer, T.I. 1925. A synopsis of the Amphibia of California. University of California Publications in Zoology 27:1-342.

Earliest publication including some basic information on CTS biology, descriptions of embryos and larvae, and natural history.

- Trenham, P.C., H.B. Shaffer, W.D. Koenig and M.R. Stromberg. 2000. Life history and demographic variation in the California tiger salamander (*Ambystoma californiense*). Copeia 2000:365-377.

Seven year study of CTS in one ephemeral constructed livestock pond in Monterey County. Showed that <5% of embryos survived to metamorphosis, that reproduction varied dramatically year to year, that <10% of metamorphs survived to breed, that most required 4 or 5 years before breeding for the first time, that annual adult probability of survival was roughly 60%, and that some lived 11 years or longer. Note: Pete's suggestion that this pond was a sink incapable of sustaining a population in the long-term was later found to be flawed.

- Trenham, P.C. 2001. Terrestrial habitat use by adult California tiger salamanders. Journal of Herpetology 35:343-346.

Using radio tracking, emigration of adults was followed after breeding for up to 4 months. All animals tracked used ground squirrel burrows. Average distance moved was about 100 m. One of the 11 animals was tracked to a burrow 248 m from the pond where it bred. Movements on rainy nights were considerably longer than those on nights without rain.

- Trenham, P.C., W.D. Koenig and H.B. Shaffer. 2001. Spatially autocorrelated demography and interpond dispersal in the California tiger salamander, *Ambystoma californiense*. Ecology 82:3519-3530.

Animals marked at 10 different breeding ponds along a 3 km transect were recaptured over a period of three years. Roughly 25% of recaptured CTS were at a pond other than the one where they were originally marked. Individuals moved between ponds separated by up to 680 meters. This reflects more interpond dispersal than would have been expected previously.

- Trenham, P.C. and H.B. Shaffer. 2005. Amphibian upland habitat use and its consequences for population viability. Ecological Applications 15:158-1168.

Single season study of CTS densities in upland habitat around Olcott Lake, Solano County. Capture rates of adults was highest in traps 10 m from the pond and declined in traps farther out; subadult capture rates during the winter months were lowest at 10 m from the pond and peaked in traps 400 m out. Estimated that 95% of both subadults and adults remain within 630 m of this breeding pond, and that ponds with 600 m of intact upland habitat surrounding them will support populations near their natural capacity.

- Trenham, P.C. and D.G. Cook. 2008. Distribution of migrating adults related to the location of remnant grassland around an urban California tiger salamander (*Ambystoma californiense*) breeding pool. In R.E. Jung and J.C. Mitchell (Eds.), *Urban Herpetology*, Herpetological Conservation, Vol. 3, Society for the Study of Amphibians and Reptiles, Salt Lake City, UT.

At a breeding pond in Santa Rosa most adults were captured entering on the east side of the pond. This appears to be because substantial grassland habitat only remains in this direction. Captures did not appear to be related to the amount of grassland within 100 m of the pool but to the amounts farther away (200 – 700 m).

- Twitty, V.C. 1941. Data on the life history of *Ambystoma tigrinum californiense* Gray. Copeia 1941:1-4.

Observations of CTS in and around Lake Lagunita on the Stanford Campus. Includes counts of adults encountered along Junipero Sera Boulevard during 1939-40 breeding migrations; on first nights of the migration almost all individuals observed were males (a common observation).

- U.S. Fish and Wildlife Service (USFWS). 19 January 2000. Emergency rule to list the Santa Barbara County distinct population of the California tiger salamander as endangered. Federal Register 65(12):3096-3109. Proposal to list the Santa Barbara County distinct population of the California tiger salamander as endangered. Federal Register 65(12):3110-3111.

- U.S. Fish and Wildlife Service (USFWS). 21 September 2000. Final rule to list the Santa Barbara County distinct population of the California tiger salamander as endangered. Federal Register 65(184):57242-57264.

- U.S. Fish and Wildlife Service (USFWS). 13 June 2002. Review of species that are candidates or proposed for listing as endangered or threatened; annual notice of findings on recycled petitions; annual description of progress on listing actions. Federal Register 67(114):40657-40679.

- U.S. Fish and Wildlife Service (USFWS). 22 July 2002. Listing the Sonoma County distinct population segment of the California tiger salamander as endangered. Federal

Register 67(140):47726-47740.

- U.S. Fish and Wildlife Service (USFWS). 19 March 2003. Determination of endangered status for the Sonoma County distinct population segment of the California tiger salamander. Federal Register 68(53):13498-13520.

- U.S. Fish and Wildlife Service (USFWS). 4 August 2004. Determination of threatened status for the California tiger salamander; and special rule exemption for existing routine ranching activities; final rule. Federal Register 69(149):47212-47248.

- Wang, I. J. and H. B. Shaffer. 2017. Population genetic and field-ecological analyses return similar estimates of dispersal over space and time in an endangered amphibian. Evolutionary Applications 10: 630-639.

Genetic estimates of dispersal and population size from Hastings match previous estimates from this landscape that were based upon a mark-recapture study.

- Wang, I., H.B. Shaffer and W.K. Savage. 2009. Landscape genetics and least-cost path analysis reveal unexpected dispersal routes in the California tiger salamander (*Ambystoma californiense*). Molecular Ecology 18:1365-1374.

They gathered genetic data on animals from 16 ponds in the Fort Ord area, and found evidence supporting recent dispersal between 4 pairs of ponds separated by from 1.0 – 1.3 km. They combined the genetic data with an analysis of the upland habitat salamanders would have to cross between these 4 pairs of ponds. This analysis suggested that CTS travel most easily through chaparral. Travel across grassland appears to be twice as costly, and through oak woodland five times more costly.

- Wang, I., J.J. Johnson, B.B. Johnson and H.B. Shaffer. 2011. Effective population size is strongly correlated with breeding pond size in the endangered California tiger salamander (*Ambystoma californiense*). Conservation Genetics 12:911-920.

Effective population size is positively correlated with breeding pond size for natural vernal pools, but not for stock ponds.

- Wilcox, J.T. G.E. Padgett-Flohr, J.A. Alvarez, and J.R. Johnson. 2015. Possible phenotypic influence of superinvasive alleles on larval California tiger salamanders (*Ambystoma californiense*). American Midland Naturalist 173:168-175.

Alvarez (2004) found, in Contra Costa County, what were thought to be CTS larvae from the prior year still present as larvae during the next winter. A new genetic assessment of this population and another population with abberant larvae (Santa Clara County) indicates that these populations both show some amount of non-native alleles. This means they are hybrids.

Some Useful Websites:

California Department of Fish and Wildlife Non-Game Wildlife Program Publications
http://www.dfg.ca.gov/wildlife/nongame/publications/

Nature Serve – background summary for CTS
http://www.natureserve.org/explorer/

California Herps – online directory of species descriptions and lots of photos
www.californiaherps.com

Survey Guidelines – released jointly by USFWS and CDFW
http://www.fws.gov/sacramento/ES/Survey-Protocols-Guidelines/es_survey.htm

Sacramento Fish and Wildlife Office – Information regarding minimum qualifications for obtaining a recovery permit for CTS and other species
http://www.fws.gov/cno/es/minqual.html

Shaffer Lab Webpage – Access to most publications by Brad Shaffer and collaborators
https://www.eeb.ucla.edu/Faculty/Shaffer/

Some Suppliers:

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