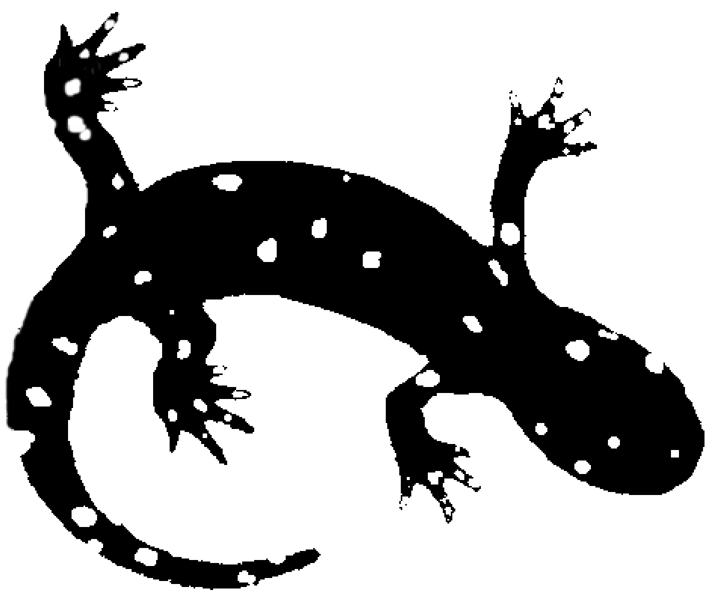
WORKSHOP

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



Workshop Leader: Pete Trenham

Timeline of Events in 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 suggested 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 as endangered

2004 USFWS list Central distinct population segment as threatened

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

2010 California Department of Fish and Game lists CTS as threatened throughout range

Glossary of Terminology Used

Adult – A tiger salamander that is capable of breeding. Breeding adult males are identifiable by their swollen vent and an 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, lungs develop, 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. tigrinum* 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 4/2009)

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

Although *A. tigrinum* 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 *Hyla 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(2):145-153.

- 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.

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

- 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.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 show 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.

- 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 modi. ed 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.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. tigrinum* were introduced by bait dealers, hybrids of *A. tigrinum* and *A. californiense* are now present. Genetic assays indicated that salamanders present in permanent constructed ponds contained greater proportions of *A. tigrinum* 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.

- 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. Geographic Distribution. *Ambystoma californiense*. Herpetol. Rev., 27(3): 147.

- Jennings, M.R. 1996. *Ambystoma californiense*. Burrowing Ability. Herpetol. Rev., 27(4): 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. et al. 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. tigrinum* exist in northern and southern California and in the Sierra Nevada. Populations of tiger salamanders near the Oregon border are potentially native *A. tigrinum* as they are most closely releated to Washington populations.

- 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 burrow 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.

- 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 large number of adult and subadult CTS on the order of 1000m 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 of 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. Source: 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.

- 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 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. tigrinum.* Populations studied were in the Salinas Valley, Monterey County.

- 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 than occurred in the area around ponds without die-offs.

- 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.

- 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.

- 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.

● Stebbins, R.C. 1985. A field guide to western reptiles and amphibians. Second edition. Houghton Mifflin Company, Boston, Massachusetts. xiv + 336 pp.

● 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. 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. & Cook, D. G. 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 & J.C. Mitchell (Eds.), *Urban Herpetology*, Herpetological Conservation, Vol. 3, Society for the Study of Amphibians and Reptiles, Salt Lake City, UT, USA.

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).

- 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 3km 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., 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: my 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. 1998. Demography, migration, and metapopulation structure of pond breeding salamanders. Ph.D. dissertation, University of California, Davis. 96 pp.

The information in chapters 1 and 2 is largely found in the above papers: Trenham et al. (2000, 2001)

- 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. 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

Some Useful Websites:

California Department of Fish and Game 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 FWS and CDFG
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
http://www2.eve.ucdavis.edu/shafferlab/

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