

California Tiger Salamander (*Ambystoma californiense*)

Status

State: Species of Special Concern

Federal: Threatened (U.S. Fish and Wildlife Service 2004a, 2004b, 2005)



Population Trend

Global: California State endemic; declining (Jennings and Hayes 1994)

State: Declining (Jennings and Hayes 1994)

Within Inventory Area: Unknown

Data Characterization

The location database for the California tiger salamander (*Ambystoma californiense*) within the inventory area includes 96 data records dated from 1920 to 1999. Of these records, 45 were documented within the past 10 years. Of the 45 records, all are considered extant, and 37 are mapped at a “specific” precision level (within 80 meters).

There is a moderate amount of general information on the ecology of the California tiger salamander and several peer-reviewed research studies. Available literature includes research on reproductive ecology, burrowing ability, dispersal from breeding area, habitat use and migratory behavior. There are many gaps in data for the California tiger salamander, including habitat and population distribution, and differentiating between introduced tiger salamanders and California tiger salamanders. The lack of certain types of data may be due to the fact that this species spends most of its life underground in small mammal burrows (U.S. Fish and Wildlife Service 2000). The California tiger salamander was not recognized as distinct species until 1991 (U.S. Fish and Wildlife Service 2000).

Range

The California tiger salamander is endemic to California. Historically, the California tiger salamander probably occurred in grassland habitats throughout much of the state. Although this species still occurs within much of its range, it has been extirpated from many historic localities (Fisher and Shaffer 1996, Stebbins 1985). The loss of California tiger salamander populations has been due primarily to habitat loss within its historic range (Fisher and Shaffer 1996).

Currently, the California tiger salamander occurs in six populations from the Central Valley and Sierra Nevada foothills, from Yolo County south to Tulare County, and in the coastal valleys and foothills, from Sonoma County south to Santa Barbara County (Zeiner et al. 1988).

The six populations of California tiger salamander are found in Sonoma County, Santa Barbara County, the Bay Area (central and southern Alameda County, Santa Clara County, western Stanislaus and Merced Counties, and San Benito County), the Central Valley (Yolo County, Sacramento County, East Contra Costa County, northeast Alameda County, San Joaquin County, Stanislaus County, Merced County and northwest Madera County), southern San Joaquin Valley (Madera County, central Fresno County, northern Tulare County, and Kings County), and the Central Coast Range (south Santa Cruz County, Monterey County, northern San Luis Obispo County, western San Benito, Fresno and Kern Counties) (U.S. Fish and Wildlife Service 2003a). Isolated populations are found at the Gray's Lodge Wildlife Area in Butte County and at Grass Lake in Siskiyou County (Zeiner et al. 1988). Most populations occur at elevations below 1,500 feet, but tiger salamanders have been recorded at elevations up to 4,500 feet. Although populations have declined, the species continues to breed at a large number of locations within its current range (59 FR 18353–18354, April 18, 1994). At most historic breeding sites below 200 feet elevation, ponds remain present but no longer support California tiger salamanders. These sites are typically occupied by non-native species (Fisher and Shaffer 1996).

Occurrences within the ECCC HCP Inventory Area

Because a comprehensive survey for the California tiger salamander has not been conducted in the HCP inventory area, neither the current population size nor the locations of all occurrences are known.

Biology

Habitat

California tiger salamanders require 2 major habitat components: aquatic breeding sites and terrestrial estivation or refuge sites. California tiger salamanders inhabit valley and foothill grasslands and the grassy understory of open woodlands, usually within 1 mile of water (Jennings and Hayes 1994). The California tiger salamander is terrestrial as an adult and spends most of its time underground in subterranean refugia. Underground retreats usually consist of ground-squirrel burrows and occasionally human-made structures. Adults emerge from underground to breed, but only for brief periods during the year. Tiger salamanders breed and lay their eggs primarily in vernal pools and other ephemeral ponds that fill in winter and often dry out by summer (Loredo et al. 1996); they sometimes use permanent human-made ponds (e.g., stock ponds), reservoirs, and small lakes that do not support predatory fish or bullfrogs (see "Ecological Relationships" discussion below) (Stebbins 1972, Zeiner et al. 1988). Streams are rarely used for reproduction.

Adult salamanders migrate from upland habitats to aquatic breeding sites during the first major rainfall events of fall and early winter and return to upland habitats after breeding. This species requires small-mammal (e.g., California ground squirrel) burrows for cover during the non-breeding season and during migration to and from aquatic breeding sites (Zeiner et al. 1988). Petranka (1998) estimated that 83% of California tiger salamanders utilize rodent burrows for upland refugia (*in* U.S. Fish and Wildlife Service 2003). California tiger salamanders also use logs, piles of lumber, and shrink-swell cracks in the ground for cover (Holland et al. 1990). California tiger salamanders can overwinter in burrows up to 1 mile from their breeding sites (Jennings and Hayes 1994).

The California tiger salamander is particularly sensitive to the duration of ponding in aquatic breeding sites. Because tiger salamanders have a long developmental period, the longest lasting seasonal ponds or vernal pools are the most suitable type of breeding habitat for this species; these pools are also typically the largest in size (Jennings and Hayes 1994). Because at least 10 weeks are required to complete metamorphosis (see “Demography” below) (Feaver 1971), aquatic sites that are considered suitable for breeding should at least pond or retain water for a minimum of 10 weeks. Moreover, large vernal pool complexes, rather than isolated pools, probably offer the best quality habitat; these areas can support a mixture of core breeding sites and nearby refuge habitat (Shaffer et al. 1994, Jennings and Hayes 1994).

The suitability of California tiger salamander habitat is proportional to the abundance of upland refuge sites that are near aquatic breeding sites. California tiger salamanders primarily use California ground squirrel burrows as refuge sites (Loredo et al. 1996; Trenham 2001); Botta’s pocket gopher burrows are also frequently used (Barry and Shaffer 1994, Jennings and Hayes 1994). The presence and abundance of tiger salamanders in many areas are limited by the number of small-mammal burrows available; salamanders are typically absent from areas that appear suitable other than their lack of burrows. Loredo et al. (1996) emphasized the importance of California ground squirrel burrows as refugia for California tiger salamanders, and suggested that a commensal relationship existed between the California tiger salamander and California ground squirrel in which tiger salamanders benefit from the burrowing activities of squirrels. In a study conducted near Concord, California, Loredo et al. (1996) found that California ground squirrel burrows were used almost exclusively as refuge sites by California tiger salamanders. Also, tiger salamanders apparently do not avoid burrows occupied by ground squirrels (Loredo et al. 1996).

The proximity of refuge sites to aquatic breeding sites also affects the suitability of salamander habitat. Although the variation in distances between breeding and refuge sites is poorly studied (Jennings and Hayes 1994), juvenile salamanders are known to migrate distances up to 1 mile (1.6 km) from breeding sites (Austin and Shaffer 1992, Mullen *in* U.S. Fish and Wildlife Service 2000). Loredo et al. (1996) found that tiger salamanders may use burrows that are first encountered during movements from breeding to upland sites. In their study area, where the density of California ground squirrel burrows was high, the average migration distances between breeding and refuge sites for adults and juveniles was 118 feet (35.9 m) and 85 feet (26.0 m), respectively. Therefore, although salamanders may migrate up to 1 mile, migration distances are likely to be less in areas

supporting refugia closer to breeding sites. Also, habitat complexes that include upland refugia relatively close to breeding sites are considered more suitable because predation risk and physiological stress in California tiger salamanders probably increases with migration distance.

Reproduction

Adult California tiger salamanders migrate to and congregate at aquatic breeding sites during warm rains, primarily between November and February (Shaffer and Fisher 1991, Barry and Shaffer 1994). Tiger salamanders are rarely observed except during this period (Loredo et al. 1996). During this period, tiger salamanders breed and lay eggs primarily in vernal pools and other shallow ephemeral ponds that fill in winter and often dry by summer (Loredo et al. 1996). Spawning usually occurs within a few days after migration, and adults probably leave the breeding sites at night soon after spawning (Barry and Shaffer 1994 citing Storer 1925).

Eggs are laid singly or in clumps on both submerged and emergent vegetation and on submerged debris in shallow water (Stebbins 1972, Shaffer and Fisher 1991, Barry and Shaffer 1994, Jennings and Hayes 1994). Larvae develop rapidly, and metamorphosis begins in late spring or early summer (Loredo-Prendeville 1995). At least 10 weeks are required to complete metamorphosis (Feaver 1971). Juveniles disperse from aquatic breeding sites to upland habitats after metamorphosis (Storer 1925, Holland et al. 1990).

California tiger salamanders breed in vernal pools and other temporary rainwater ponds. This species will also use permanent human-made ponds, without predatory fish, for reproduction. Females lay eggs on submerged vegetation in shallow water. In ponds without vegetation, females will lay eggs on objects on the pond bottom (Jennings and Hayes 1994). After breeding, adults leave the breeding ponds and return to small mammal burrows.

After approximately 2 weeks, the salamander eggs begin to hatch into larvae. Once larvae reach a minimum body size they metamorphose to the terrestrial juvenile salamander. Larvae in small ponds develop faster, while larvae inhabiting ponds that retain water for longer will be larger at time of metamorphosis. In general, salamanders require 10 weeks living in ponded water for complete metamorphosis. If a pond dries prior to metamorphosis, the larvae will desiccate and die (U.S. Fish and Wildlife Service 2000).

The California tiger salamander breeds primarily in vernal pools and swales—unique ecosystems that fill with winter rains and dry completely by summer—and then spends most of its lifecycle estivating underground in adjacent valley oak woodland or grassland habitat, primarily in abandoned rodent burrows. Research has shown that dispersing juveniles can roam up to 1 mile from their breeding ponds and that a minimum of 480 acres of uplands habitat is needed surrounding a breeding pond in order for the species to survive over the long term. Reserves of multiple breeding ponds surrounded by 1000 acres or more of habitat are recommended to ensure the persistence of the species.

Foraging Requirements

Aquatic larvae feed on algae, small crustaceans, and small mosquito larvae for about 6 weeks after hatching (U.S. Fish and Wildlife Service 2000). Larger larvae feed on zooplankton, amphipods, mollusks, and smaller tadpoles of Pacific treefrogs, red-legged frogs, western toads and spadefoot toads (Zeiner et al. 1988, U.S. Fish and Wildlife Service 2000). During estivation, California tiger salamanders eat very little (Shaffer et al. 1994 in U.S. Fish and Wildlife Service 2000). During the fall and winter, adult salamanders emerge from underground retreats during rain events and on nights of high relative humidity to feed and migrate to breeding ponds (U.S. Fish and Wildlife Service 2000). Adults eat earthworms, snails, insects, fish, and small mammals (Stebbins 1972).

Demography

Local populations of California tiger salamanders may not reproduce during years of low rainfall when ephemeral pools do not fill (Barry and Shaffer 1994, Jennings and Hayes 1994). However, it is presumed that the longevity of this species allows local populations to persist through all but the longest drought periods (Barry and Shaffer 1994). Individuals have been known to live for more than 10 years (Trenham et al. 2000 in U.S. Fish and Wildlife Service 2000).

Trenham et al. (2001) showed that pool complexes occupied by California tiger salamander fit a metapopulation model. Also, long-term demographic data suggest that there are source-sink relationships between pools in a complex (Trenham et al. 2000, 2001) (see “Dispersal” below).

Dispersal

Adult California tiger salamanders migrate to and congregate at aquatic breeding sites during warm rains, primarily between November and February (Shaffer and Fisher 1991, Barry and Shaffer 1994). Tiger salamanders are rarely observed except during this period (Loredo et al. 1996). Dispersal of juveniles from natal ponds to underground refugia occurs during summer months, when breeding ponds dry out. Juveniles disperse from breeding sites after spending a few hours or days near the pond margin (Jennings and Hayes 1994). Dispersal distance varies and may increase with an increase in precipitation (Trenham in revision in U.S. Fish and Wildlife Service 2000). Juveniles have been found more than 1,200 feet away from breeding ponds (Mullen in U.S. Fish and Wildlife Service 2000), yet most juveniles tend to remain closer to breeding ponds (U.S. Fish and Wildlife Service 2000; Shaffer and Trenham in press).

Some genetic data suggest low rates of California tiger salamander migration between vernal pool complexes (Shaffer et al. 1994, Irschick and Shaffer 1997) or metapopulations; this suggests that natural colonization after a local extirpation event may be unlikely (Fisher and Shaffer 1994). Trenham et al. (2001) showed that pool complexes occupied by California tiger salamander fit a metapopulation model, and dispersal rates between ponds may be high for both

first-time and experienced breeders; and dispersal rates are probably high enough to prevent local extirpations within a pool complex.

Ecological Relationships

California tiger salamander larvae and embryos are susceptible to predation by fish (Stebbins 1972, Zeiner et al. 1988, Shaffer et al. 1994), and tiger salamander larvae are rarely found in aquatic sites that support predatory fish (Shaffer and Fisher 1991, Shaffer and Stanley 1992, Shaffer et al. 1994). Aquatic larvae are taken by herons and egrets and possibly garter snakes (Zeiner et al. 1988). Shaffer et al. (1993) also found a negative correlation between the occurrence of California tiger salamanders and the presence of bullfrogs; however, this relationship was detected only in unvegetated ponds. This suggests that vegetation structure in aquatic breeding sites may be important for survival. Because of their secretive behavior and limited periods above ground, adult California tiger salamanders have few predators (U.S. Fish and Wildlife Service 2000).

Threats

California tiger salamander populations have experienced dramatic declines throughout the historical range of the species, particularly in the Central Valley. California tiger salamander populations have declined as a result of 2 primary factors: widespread habitat loss and habitat fragmentation. These factors have both been caused by conversion of valley and foothill grassland and oak woodland habitats to agricultural and urban development (Stebbins 1985). For example, residential development and land use changes in the California tiger salamander's range have removed or fragmented vernal pool complexes, eliminated refuge sites adjacent to breeding areas, and reduced habitat suitability for the species over much of the Central Valley (Barry and Shaffer 1994, Jennings and Hayes 1994). Grading activities have probably also eliminated large numbers of salamanders directly (Barry and Shaffer 1994). Overall, approximately 75% of habitat for California tiger salamander within its historic range has been lost (Fisher and Shaffer 1996).

The introduction of bullfrogs, Louisiana red swamp crayfish, and non-native fishes (mosquitofish, bass, and sunfish) into aquatic habitats has also contributed to declines in tiger salamander populations (Jennings and Hayes 1994; 59 FR 18353–18354, April 18, 1994, U.S. Fish and Wildlife Service 2000). These non-native species prey on tiger salamander larvae and may eliminate larval populations from breeding sites (Jennings and Hayes 1994). At sites where aquatic vegetation is present, exotic fish appear more likely to result in California tiger salamander extirpation than bullfrogs (Fisher and Shaffer 1996). At most historic breeding sites below 200 feet elevation, ponds remain present but no longer support California tiger salamanders. Instead, these sites are typically occupied by non-native species (Fisher and Shaffer 1996).

Burrowing-mammal control programs are considered a threat to California tiger salamander populations. Rodent control through destruction of burrows and release of toxic chemicals into burrows can cause direct mortality to individual salamanders and may result in a decrease of available suitable habitat (U.S. Fish and Wildlife Service 2000).

Vehicular related mortality is an important threat to California tiger salamander populations (Barry and Shaffer 1994, Jennings and Hayes 1994). California tiger salamanders will readily attempt to cross roads during migration, and roads that sustain heavy vehicle traffic or barriers that impede seasonal migrations may have impacted tiger salamander populations in some areas (Shaffer and Fisher 1991, Shaffer and Stanley 1992, Barry and Shaffer 1994). Therefore, establishing artificial structures that could impede movements or maintaining roads that support a considerable amount of vehicle traffic in areas that support California tiger salamander populations can severely degrade salamander habitat (see Jennings and Hayes 1994).

Hybridization between California tiger salamander and an introduced congener, *A. tigrinum*, has been documented and may be extensive (Riley et al. 2003). *A. tigrinum* was introduced to California for use as fishing bait; and both taxa co-occur in ponds and vernal pools. Hybridization between native and exotic taxa, due to lack of reproductive isolation, can threaten native taxa by causing genetic swamping, reduced genetic diversity, and reduced genetic purity of native populations. In rare species such as California tiger salamander, hybridization can also lead to population extirpation. In a study of tiger salamander hybridization conducted in the Salinas Valley, Riley et al. (2003) found that the degree of genetic mixing between California tiger salamander and *A. tigrinum* depended on breeding habitat type. In artificial ponds, there appeared to be no barriers to gene exchange between California tiger salamander and *A. tigrinum*. However, in vernal pools, significantly fewer hybrid genotypes and more pure parental genotypes were found. These results suggest that the potential for reproductive isolation between the two taxa may be higher in native habitats.

Conservation and Management

The California tiger salamander is a Federal threatened species and California Species of Special Concern within the ECCC HCP/NCCP inventory area (U.S. Fish and Wildlife Service 2004a). The recent listing by the U.S. Fish and Wildlife Service strongly indicates the imperiled nature of this species. The East Bay and Livermore Valley populations comprise a genetically distinct region within the California tiger salamander's distribution (Shaffer et al. 1994; U.S. Fish and Wildlife Service 2005). Also, the East Bay and Sacramento Valley populations may be the most genetically diverse populations, suggesting that those regions may comprise the core of the species' distribution, and are of particularly high conservation value (Shaffer et al. 1994; U.S. Fish and Wildlife Service 2005).

Existing conservation measures for this species include preservation of occupied habitat, replacement or enhancement of lost breeding habitat, and prevention of

contamination of aquatic habitat used by the species. Research has shown that dispersing juveniles can roam up to 1 mile from their breeding ponds and that a minimum of 480 acres of uplands habitat is needed surrounding a breeding pond in order for the species to survive over the long term. Reserves of multiple breeding ponds surrounded by 1,000 acres or more of habitat are recommended to ensure the persistence of the species (Center for Biological Diversity 2002).

Modeled Species Distribution

Model Description

Assumptions

1. All ponds, wetlands, seasonal wetlands, and alkali wetlands within annual grassland, oak savanna, and oak woodland were considered potential breeding habitat for California tiger salamander.
2. All non-urban, non-aquatic land cover types within 1 mile of potential breeding sites were considered potential migration and aestivation habitat for this species.

Rationale

California tiger salamanders require 2 major habitat components: aquatic breeding sites and terrestrial aestivation or refuge sites. California tiger salamanders inhabit valley and foothill grasslands and the grassy understory of open woodlands, usually within 1 mile of water (Jennings and Hayes 1994). The California tiger salamander is terrestrial as an adult and spends most of its time underground in subterranean refugia. Underground retreats usually consist of ground-squirrel burrows and occasionally human-made structures. Adults emerge from underground to breed, but only for brief periods during the year. Tiger salamanders breed and lay their eggs primarily in vernal pools and other ephemeral ponds that fill in winter and often dry out by summer (Loredo et al. 1996); they sometimes use permanent human-made ponds (e.g., stock ponds), reservoirs, and small lakes that do not support predatory fish or bullfrogs (see “Ecological Relationships” discussion below) (Stebbins 1972, Zeiner et al. 1988). Streams are rarely used for reproduction.

Adult salamanders migrate from upland habitats to aquatic breeding sites during the first major rainfall events of fall and early winter and return to upland habitats after breeding. This species requires small-mammal (e.g., California ground squirrel) burrows for cover during the non-breeding season and during migration to and from aquatic breeding sites (Zeiner et al. 1988). California tiger salamanders also use logs, piles of lumber, and shrink-swell cracks in the ground for cover (Holland et al. 1990) California tiger salamanders can overwinter in burrows up to 1 mile from their breeding sites (Jennings and Hayes 1994).

The proximity of refuge sites to aquatic breeding sites also affects the suitability of salamander habitat. Although the variation in distances between breeding and refuge sites is poorly studied (Jennings and Hayes 1994) juvenile salamanders are known to migrate distances up to 1 mile (1.6 km) from breeding sites (Austin

and Shaffer 1992, Mullen *in* U.S. Fish and Wildlife Service 2000. Research has shown that dispersing juveniles can roam up to 1 mile from their breeding ponds.

Model Results

Figure 2 shows the modeled potential habitat of the California tiger salamander. The habitat includes approximately two-thirds of the inventory area and is largely located in the hilly portions of the western side of this area. All documented occurrences of this species fit well within the boundaries of the model.

The large proportion of the modeled habitat within non-urban areas is due to the large number of ponds that provide potential breeding habitat and the potential dispersal distance of this species. Loredó et al. (1996) found that tiger salamanders may use burrows that are first encountered during movements from breeding to upland sites. In their study area, where the density of California ground squirrel burrows was high, the average migration distances between breeding and refuge sites for adults and juveniles was 118 feet (35.9 m) and 85 feet (26.0 m), respectively. Therefore, although salamanders may migrate up to 1 mile, migration distances are likely to be less in areas supporting refugia closer to breeding sites. However, because the actual movement patterns of the salamanders away from breeding sites is not known within the inventory area, we used a conservative estimate of 1 mile to define the potential movement/dispersal habitat requirements for this species. Also, due to the 10 acre minimum resolution function of the model, vernal pools and seasonal wetlands could not be delineated within the modeled distribution area and their abundance is likely to have been underestimated.

Literature Cited

- Austin, C. C., and H. B. Shaffer. 1992. *Short-, medium-, and long-term repeatability of locomotor performance in the tiger salamander Ambystoma californiense*. *Functional Ecology* 6:145–153.
- 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.
- Center for Biological Diversity. 2002. Center moves to protect vanishing amphibian under both federal and Californian Endangered Species Acts. Available at: (<http://www.biologicaldiversity.org/swcbd/species/ctigersal/>).
- Feaver, P. E. 1971. Breeding pool selection and larval mortality of three California amphibians: *Ambystoma tigrinum californiense* Gray, *Hyla regilla* Baird and Girard, and *Scaphiopus hammondi* Girard. MA Thesis, Fresno State College, Fresno, CA.
- Fisher, R. N. and H. B. Shaffer. 1996. The decline of amphibians in California's Great Central Valley. *Conservation Biology* 10:1387-1397.

- 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.
- Irschick, D. J. and H. B. Shaffer. 1997. The polytypic species revisited: morphological differentiation among tiger salamanders (*Ambystoma tigrinum*) (Amphibia: Caudata). Herpetologica 53:30–49.
- Jennings, M. R., and M. P. Hayes. 1994. Amphibian and reptile species of special concern in California. Final Report to the California Department of Fish and Game, Inland Fisheries Division, Rancho Cordova, CA. 225 pp.
- Loredo, I., D. Van Vuren, and M. L. Morrison. 1996. *Habitat use and migration behavior of the California tiger salamander*. Journal of Herpetology 30:282–285.
- Loredo-Prendeville, I. 1995. Reproductive ecology, microhabitat use, and migration behavior of the California tiger salamander. Unpubl. M.S. Thesis, University of California, Davis.
- Riley, S. P. D., H. B. Shaffer, 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.
- Shaffer, H. B., and R. Fisher. 1991. Final report to the California Department of Fish and Game; California tiger salamander surveys, 1990–Contract (FG 9422). California Department of Fish and Game, Inland Fisheries Division, Rancho Cordova, California.
- Shaffer, H. B., and S. Stanley. 1992. Final report to California Department of Fish and Game; California tiger salamander surveys, 1991–Contract (FG 9422). California Department of Fish and Game, Inland Fisheries Division, Rancho Cordova, California.
- Shaffer, H. B. and P. C. Trenham. In press. *Ambystoma californiense*. Pp. 1093–1102. In Lannoo, M.J. (Ed.), Status and Conservation of U.S. Amphibians. Volume 2: Species Accounts. University of California Press, Berkeley, California.
- Shaffer, H. B., R. N. Fisher, and S. E. Stanley. 1994. Status report: The California tiger salamander (*Ambystoma californiense*). Final report to the California Department of Fish and Game, Inland Fisheries Division, Rancho Cordova, California, under Contracts (FG 9422 and FG 1383).
- Stebbins, R. C. 1972. *California amphibians and reptiles*. Univ. California Press, Berkeley. 152 pp.
- Stebbins, R. C. 1985. *A field guide to western reptiles and amphibians*. Second edition, revised. Houghton Mifflin Company, Boston, MA.

- Storer, T. I. 1925. *A synopsis of the amphibia of California*. Univ. California Publ. Zool. 27: 1–342.
- 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., H. B. Shaffer, W. D. Koenig, and M. R. Stromberg. 2000. Life history and demographic variation in the California tiger salamander (*Ambystoma californiense*). *Copeia* 2:365-377.
- U.S. Fish and Wildlife Service. 2000. Endangered and threatened wildlife and plants; final determination of endangered status for the Santa Barbara County Distinct Vertebrate Population Segment of the California Tiger Salamander (*Ambystoma californiense*).
- U.S. Fish and Wildlife Service. 2003. Endangered and threatened wildlife and plants; determination of endangered status for the Sonoma County Distinct Population Segment of the California Tiger Salamander; Final Rule. 68 FR 53:13497-13520 (March 19, 2003).
- U.S. Fish and Wildlife Service. 2004a. Endangered and threatened wildlife and plants; determination of threatened status for the California Tiger Salamander; and special rule exemptions for existing routine ranching activities; Final Rule. 69 FR 149:47212-47248 (August 4, 2004).
- U.S. Fish and Wildlife Service. 2004b. Designation of critical habitat for the California tiger salamander, Proposed Rule. Federal Register 69, No. 153. August 10.
- U.S. Fish and Wildlife Service. 2005. Designation of critical habitat for the California tiger salamander, Proposed Rule. Federal Register 70, No. 162. August 23.
- Zeiner, D. C., W. F. Laudenslayer, Jr., and K. E. Meyer. 1988. *California's wildlife. Volume I: amphibians and reptiles*. May 2, 1988. California Department of Fish and Game. Sacramento, CA.