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Ambystoma californiense Gray, 1853
California Tiger Salamander

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1. Historical versus Current Distribution.

California tiger salamanders (*Ambystoma californiense*) are a California endemic with their range centered in the Central Valley from Tulare and San Luis Obispo counties in the south, to Sacramento and Solano counties in the north. They are known from sites in the bottom of the Central Valley up to a maximum elevation of roughly 1,200 m in the Coast Ranges, and 500 m in the Sierra Nevada foothills. Although the historical distribution of California tiger salamanders is not known in detail, their current distribution and genetic data suggest that they were distributed continuously in the vernal pool/grassland habitat that dominated much of this region. In addition, there are two well-characterized disjunct populations of California tiger salamanders. To the northwest of their main range there are populations near Santa Rosa, Sonoma County; to the southwest there are populations in the Santa Maria region of northwestern Santa Barbara County (Storer, 1925; Jennings and Hayes, 1994a; Fisher and Shaffer, 1996). Genetic data indicate that the Sonoma and Santa Barbara populations have been isolated from the remainder of the range for sufficient time (on the order of 1,000,000 yr) that they may represent distinct species (H.B.S., unpublished data).

The northernmost California tiger salamander specimens on record are from the California Department of Fish and Game Refuge at Grey Lodge, Butte and Sutter counties (California Department of Fish and Game, 2002). The southernmost record is for specimens collected in 1892 in Riverside County, although this record is > 300 km from the nearest known population and may represent a misidentification. In both cases, repeated surveys over the past two decades have failed to relocate these populations and they are presumed extirpated or in error (Jennings and Hayes, 1994a). Presently the northernmost population of California tiger salamander is in the vicinity of Dunnigan, Yolo County, and the southernmost populations are in Santa Barbara County. In addition to the loss of populations at the extremes of the species' range, extensive habitat conversion has extirpated many populations in the continuous portions of their range (Barry and Shaffer, 1994; Jennings and Hayes, 1994a; Fisher and Shaffer, 1996). Holland (1978) estimated that by 1973, 60–85% of natural vernal pool habitats had been lost, and what remains is increasingly fragmented by urban and agricultural development. Presently, few populations are known from sites in the Central Valley, and most recent records are for sites in the surrounding hills to the east and west (California Department of Fish and Game, 2002), presumably due to the nearly complete conversion of the Central Valley to intensive agriculture. Surveys conducted in the early 1990s failed to find any California tiger salamanders at 56% of 86 historical localities (H.B.S., unpublished data). Due to the rapid expansion of agricultural, urban development and the loss of breeding ponds in Sonoma and Santa Barbara counties, the U.S. Fish and Wildlife Service listed these distinct population segments as Endangered (U.S.F.W.S., 2000b, 2002c).

2. Historical versus Current Abundance.

California tiger salamander populations can fluctuate widely both among years and among ponds within years. At one study site in Monterey County, the number of breeding adults visiting a pond varied from 57–244 individuals, with female breeders varying by an order of magnitude among years (16–140; Trenham et al., 2000). A breeding site approximately 200 km to the north (Contra Costa County) showed a similar pattern of variation, suggesting that such fluctuations are typical (Loredo and Van Vuren, 1996). At the local landscape level, nearby breeding ponds can vary by at least an order of magnitude in the number of individuals visiting a pond, and these differences appear to be stable across years (Trenham et al., 2001). Virtually nothing is known concerning the historical abundance of the species. Twitty (1941) reported that on two rainy nights in January 1940, 28 and 45 migrating adults were obtained on the road bordering Lake Lagunita, Stanford University, Palo Alto; similar breeding migrations have been observed in recent years (A. Launer, personal communication).

3. Life History Features.

A. Breeding.

Reproduction is aquatic.

i. Breeding migrations.

Migrations to and from breeding ponds occur during the rainy season (November–May), with the greatest activity from December–February (Storer, 1925; Loredo and Van Vuren, 1996; Trenham et al., 2000). Breeding may occur in one major bout or during a prolonged period of several months, depending on the rainfall pattern (Loredo and Van Vuren, 1996; Trenham et al., 2000). Breeding migrations are strongly associated with rainfall events (Loredo and Van Vuren, 1996; Trenham et al., 2000). During drought years, adults (particularly females) migrate in low numbers. Males consistently arrive at the breeding pond before females and stay approximately four times longer—over a 7-yr period the average time spent in one Monterey County breeding pond was 44.7 d for males and 11.8 d for females (Trenham et al., 2000); Loredo and Van Vuren (1996) found similar results in a 2-yr study in Contra Costa County (males—37 d, females—10 d).

ii. Breeding habitat.

California tiger salamanders breed in fishless, seasonal and semi-permanent wetlands (Barry and Shaffer, 1994; Petranka, 1998). Historically, California tiger salamanders probably relied exclusively on shallow vernal pools for breeding habitat, but they now make extensive use of ponds constructed for cattle, particularly in foothill habitat. In Monterey County, ponds utilized as breeding habitat were natural vernal pools and artificial cattle ponds ranging in depth from 30 cm to > 2 m and ranging in annual hydroperiod from 10–52 wk (Trenham et al., 2001).

B. Eggs.

i. Egg deposition sites.

Females lay eggs singly or, more rarely, in clusters of 2–4 eggs, attached to live vegetation or detritus (Storer, 1925; Twitty, 1941). Eggs are about 3.5 mm in diameter and hatch 2–4 wk after being laid (Storer, 1925).

ii. Clutch size.

Eleven females from Monterey County contained an average of 814 eggs (range: 413–1,340; Trenham et al., 2000).

C. Larvae/Metamorphosis.

i. Length of larval stage.

Average is 4–5 mo (range 3–6), with peak laying in January and peak emergence of newly metamorphosed animals from mid June to mid July (Loredo and Van Vuren, 1996; Trenham et al., 2000). Total annual production of metamorphic animals ranged from 122–775 (4.7–21.9/female) at a Monterey County pond (Trenham et al., 2000). Newly metamorphosed individuals from three sites across the species range are fairly consistent in size (mean SVLs are 58 mm, 64 mm, and 62.4 mm; Holland et al., 1990; Loredo and Van Vuren, 1996; Trenham et al., 2000).

ii. Larval requirements.

a. Food.

Newly hatched larvae begin feeding after a few days. Larvae are gape-limited predators. Smaller larvae feed primarily on zooplankton (cladocerans and copepods); older larvae feed on tadpoles (primarily of Pacific treefrogs; *Pseudacris regilla*), ostracods, amphipods, midge larvae, water boatmen (Corixidae), and pond snails (Anderson, 1968).

b. Cover.

When not feeding, larvae are sedentary on the bottom of wetlands. Storer (1925) noted that larvae are wary, seeking cover in vegetation when disturbed.

iii. Larval polymorphisms.

Have not been reported, although large, late-metamorphosing larvae sometimes develop large heads reminiscent of cannibal morph eastern tiger salamanders (*A. tigrinum*; H.B.S., personal observation).

iv. Features of metamorphosis.

Metamorphosis typically occurs during the dry summer, and newly metamorphosed larvae emigrate from their breeding wetlands under both wet and dry conditions (Loredo and Van Vuren, 1996; Loredo et al., 1996). Median emergence date can vary by at least 2 mo across years and invariably precedes complete pond drying by several weeks (Trenham et al., 2000). At least a few metamorphic animals continue to emigrate after the pond has completely dried (Trenham et al., 2000), presumably by using dense vegetation or cracks in the substrate as temporary daytime retreats (Loredo et al., 1996).

v. Post-metamorphic migrations.

In the first night, newly metamorphosed animals move an average of about 26 m (range 6–57 m; Loredo et al., 1996). Of 69 individuals followed, roughly half found shelter in soil cracks and half in California ground squirrel (*Spermophilus beecheyi*) burrows (Loredo et al., 1996). Laboratory studies of burst and endurance locomotor capabilities demonstrate that juveniles can travel at least 25 m without resting (Shaffer et al., 1991).

vi. Neoteny.

Has not been reported. For much of their evolutionary history, California tiger salamanders were presumably restricted to vernal pool habitats and did not have the opportunity to express a fully paedomorphic life history (Storer, 1925). As breeding sites have been enlarged and made permanent, over-summering larvae have occasionally been found (H.B.S., unpublished observations). The complete absence of sexually mature paedomorphic animals suggests that this species lacks the ability to express this life history pattern. In central California, recently discovered populations containing paedomorphic animals invariably contained introduced genotypes from non-native eastern tiger salamanders, based on mitochondrial and nuclear genetic analyses (H.B.S. and colleagues, unpublished data).

D. Juvenile Habitat.

Newly metamorphosed animals emerging from one breeding pond settled in California ground squirrel (*Spermophilus beecheyi*) burrows and soil cracks in roughly equal proportions (Loredo et al., 1996). Near Lake Lagunita at Stanford University, juveniles use the crevices in a sandbag retaining wall as terrestrial retreats (Barry and Shaffer, 1994).

E. Adult Habitat.

Adults clearly rely on rodent burrows for underground retreats—except for the brief breeding season, they spend the entire year in or near these retreats. Animals unable to gain access to underground burrows may be prone to desiccation (Loredo et al., 1996). California ground squirrel (*Spermophilus beecheyi*) and valley pocket gopher (*Thommomys bottae*) burrows are the primary source of these retreats (Barry and Shaffer, 1994; Trenham, 2001). Unlike eastern tiger salamanders, adult California tiger salamanders are able to burrow through moist soil in blocked mammal burrows (Jennings, 1996a). Adults rely heavily on ground squirrel burrows, with 83% of adults using them on their first night migrations from breeding ponds (Loredo et al., 1996). Radio-tracked adults most commonly settled in burrows in open grassland areas or beneath large oaks, with burrows in woodland areas less commonly occupied (Trenham, 2001).

F. Home Range Size.

Following breeding, radio-tracked adults migrated away from breeding ponds and initially settled in ground squirrel burrows 3–158 m away (Trenham, 2001); Loredo et al. (1996) observed similar first night emigration distances. Most of the radio-tracked salamanders moved to another or several different burrow systems farther from the pond during the 1–4 mo tracking interval. For 11 salamanders, the average final distance traveled from the pond was 114 ± 83 m (Trenham, 2001). Within individual burrow systems, salamanders frequently made short moves of < 10 m, apparently without surfacing (Trenham, 2001).

G. Territories.

Generally unknown. However, using a fiber optic scope, Semonsen (1998) observed multiple juvenile salamanders in close proximity to one another within individual burrow systems near Santa Maria, suggesting that they are not strongly territorial.

H. Aestivation/Avoiding Dessication.

Summertime conditions are extremely hot (frequently > 40 ˚C) and dry (essentially zero precipitation from June–October), and aestivation may be occurring in underground retreats. However, continued within-burrow movements through at least June by some radio-equipped adult salamanders suggest that aestivation, if it occurs, is not obligate (Trenham, 2001).

I. Seasonal Migrations.

Seasonal migrations in California tiger salamanders appear to occur only for the purpose of breeding. In years when rainfall is sparse or late, larger proportions of surviving adults, especially females, fail to migrate to breeding ponds (Loredo and Van Vuren, 1996; Trenham et al., 2000). Subadults do not appear to make any regular seasonal migrations, as they are rarely captured at or near breeding ponds (P.C.T., personal observation). There is one report of juveniles migrating to a breeding site en masse following a rare August storm (Holland et al., 1990; see also Petranka, 1998). While most individuals breed for the first time in their natal pond, 31% of males and 27% of females marked at a pond were recaptured breeding for the first time at a second pond 580 m away (Trenham et al., 2001). Within a system of 11 breeding ponds, 26% of surviving adults also dispersed to other breeding ponds in subsequent years (Trenham et al., 2001). Following breeding, adults move away from breeding ponds (see "Home Range Size" above).

J. Torpor (Hibernation).

None recorded; none expected given the mild winters that California tiger salamanders encounter.

K. Interspecific Associations/Exclusions.

According to Loredo et al. (1996), California tiger salamanders may have a commensal relationship with California ground squirrels. Radio-tracked adult salamanders were always located in close association with ground squirrel burrows (Trenham, 2001). Some burrows occupied by salamanders are simultaneously in use by ground squirrels (Semonsen, 1998; P.C.T., personal observations). Burrows of pocket gophers are also used (Barry and Shaffer, 1994; Jennings, 1996a; Trenham, 2001). Because of concerns to cattle and agriculture, California ground squirrels are currently being controlled on over 4 million ha, a management practice that may indirectly threaten California tiger salamanders (Loredo et al., 1996). Associations with burrowing mammals in flat, floodplain regions of the central valley are unknown and may differ from published studies in better drained, upland habitats.

Ponds that contain populations of exotic fishes and American bullfrogs (*Rana catesbeiana*) appear unsuitable as breeding habitat (Fisher and Shaffer, 1996; H.B.S. and colleagues, unpublished data). In a related experiment, California tiger salamander embryos suffered complete predation in a fish- and American bullfrog-free permanent pond that contained large numbers of resident adult California newts (*Taricha torosa*) and dragonfly larvae, but only light predation in a nearby temporary pond lacking these predators (P.C.T., unpublished data).

L. Age/Size at Reproductive Maturity.

Minimum age at first reproduction based on recaptures of marked juveniles is 2 yr for males and 2–3 yr for females (Loredo and Van Vuren, 1996; Trenham et al., 2000). However, most individuals at one pond in Monterey County did not reach sexual maturity until 4–5 yr of age (Trenham et al., 2000); skeletochronology estimates of breeding adult age structure confirmed these estimates. Interestingly, < 50% of individuals breed a second time during their lifetime at either their natal or any other pond (Trenham et al., 2000). Trenham et al. (2000) found sizes of breeding adults to be extremely variable, ranging from 75–130 mm SVL, and only a weak positive relationship between SVL and skeletochronological age (R < 0.4).

M. Longevity.

Skeletochronology-based age estimates for the Monterey County breeding site ranged from 2–11 yr for sexually mature individuals and did not differ between sexes (Trenham et al., 2000). Most breeding adults are 4–6-yr old; confirmation with known-age animals demonstrated that these estimates are accurate (Trenham et al., 2000).

N. Feeding Behavior.

Nothing has been published on feeding ecology of post-metamorphic juveniles or adults. Based on captive individuals, they are presumed to take a wide variety of invertebrate and small vertebrate prey.

O. Predators.

California red-legged frog (*Rana draytonii*) adults are known to eat California tiger salamander larvae (Baldwin and Stanford, 1987; see also Petranka, 1998). California ground squirrels may eat adults, although salamanders do not appear to avoid occupied ground squirrel burrows (Loredo et al., 1996; Semonsen, 1998; see also Petranka, 1998). Garter snakes (*Thamnophis* sp.) will sometimes prey heavily on larvae, and at least one adult American bullfrog was found with a newly metamorphosed tiger salamander in its stomach (H.B.S., unpublished observations). Striped skunks (*Mephitis mephitis*) and garter snakes have been observed preying on adult salamanders in pitfall traps (P.C.T., personal observations). Introduced predatory fishes and California tiger salamander larvae do not co-occur in the same ponds (Fisher, 1995), suggesting that these fishes prey heavily on larvae. In a controlled field experiment, low densities of mosquito fish (*Gambusia* sp.; 0.5 fish/m2 pond surface area) had no discernible effect on California tiger salamander hatchling growth or survival to metamorphosis. However, densities more typical of many permanent ponds (12.5 fish/m2) significantly reduced growth and survival to metamorphosis of California tiger salamander larvae (K. Leyse, unpublished data). Presumably the same types of predators that occur in eastern tiger salamander populations also influence California tiger salamanders, including predatory birds and small mammals.

P. Anti-Predator Mechanisms.

Unknown.

Q. Diseases.

Unknown.

R. Parasites.

Unknown.

4. Conservation.

California tiger salamanders are considered a Species of Special Concern across its range by the State of California. They are a candidate for listing under the U.S. Endangered Species Act, and in 1994, listing was determined to be "warranted" by the U.S. Fish and Wildlife service, but "precluded" due to higher priority species (U.S.F.W.S., 1994a). In January 2000, the Santa Barbara populations received emergency listing under the Endangered Species Act as an Endangered species (U.S.F.W.S., 2000b). In March 2003, the Sonoma County distinct population segment was listed as Endangered (Federal Register, 2003). Habitat destruction (both of breeding pools and upland terrestrial habitat) and introduced exotic predators are widely considered to be the primary causes of decline (Stebbins and Cohen, 1995; Fisher and Shaffer, 1996; Davidson, 2000; Davidson et al., 2002). Introduced *A. tigrinum* also hybridize with native *A. californiense*, causing genetic "biopollution" problems in central California (Riley et al., submitted manuscript).