

The salamanders breeding in, and living around, a seasonal pool or pools, and associated uplands where estivation can occur, are said to occupy a breeding site. A breeding site is defined as a location where the animals are able to successfully breed in years of "normal" rainfall and complete their estivation. Historically, California tiger salamanders utilized vernal pools, but the species will also breed in stockponds.

Occurrence of California tiger salamanders is significantly associated with occurrence of California ground squirrels (Seymour and Westphal 1994). Active ground burrowing rodent colonies probably are required to sustain California tiger salamanders because inactive burrow systems become progressively unsuitable over time. Loredó *et al.* (1996) found that California ground squirrel burrow systems collapsed within 18 months following abandonment by, or loss of, the mammals. Although California tiger salamanders use both occupied and unoccupied burrows, they apparently do not use collapsed burrows.

Adult California tiger salamanders may migrate up to 1.6 km (1 mi) from their upland sites to the breeding ponds (S. Sweet, University of California, Santa Barbara, *in litt.* 1998), which may be vernal pools, stockponds, or other seasonal water bodies. The distance between the upland sites and breeding pools depends on local topography and vegetation, and the distribution of California ground squirrel or other rodent burrows (Stebbins 1989). Males migrate to the breeding ponds before females (Twitty 1941; Shaffer, *et al.* 1993; Loredó and Van Vuren 1996; Trenham 1998b). Males usually remain in the ponds for an average of about 6 to 8 weeks, while females stay for approximately 1 to 2 weeks. In dry years, both sexes may stay for shorter periods (Loredó and Van Vuren 1996; Trenham 1998b). Most marked salamanders have been recaptured at the pond where they were initially captured; in one study, approximately 80 percent were recaptured at the same pond (Trenham 1998b). The rate of natural movement of salamanders among breeding sites depends on the distance between the ponds or complexes of ponds and on the quality of intervening habitat (*e.g.*, salamanders may move more quickly through sparsely covered and open grassland than they can through densely vegetated lands) (Trenham 1998a). As with migration distances, the number of ponds used by an individual over its lifetime depends on landscape features and environmental factors.

The adults mate in the ponds and the females lay their eggs in the water (Twitty 1941; Shaffer *et al.* 1993; Petranksa 1998). Females attach their eggs singly or, in rare circumstances, in groups of two to four, to twigs, grass stems, vegetation, or debris (Storer 1925; Twitty 1941). In ponds with no or limited vegetation, females may attach eggs to objects, such as rocks and boards on the bottom (Jennings and Hayes 1994). After breeding, adults leave the pool and return to the small mammal burrows (Loredó *et al.* 1996; Trenham 1998a), although they may continue to come out nightly for approximately the next 2 weeks to feed (Shaffer *et al.* 1993). In drought years, the seasonal pools may not form and the adults cannot breed (Barry and Shaffer 1994).

Salamander eggs hatch in 10 to 14 days with newly hatched salamanders (larvae) ranging in size from 11.5 to 14.2 mm (0.45 to 0.55 in) in total length (Petranksa 1998). The larvae are aquatic. Each is yellowish gray in color and has a broad fat head, large, feathery external gills, and broad dorsal fins that extend well onto its back. The larvae feed on zooplankton, small crustaceans, and aquatic insects for about 6 weeks after hatching, after which they switch to larger prey (J. Anderson 1968). Larger larvae have been known to consume smaller tadpoles of Pacific treefrogs (*Pseudacris regilla*) and California red-legged frogs (*Rana aurora*) (J. Anderson 1968; P. Anderson 1968). The larvae are among the top aquatic predators in the seasonal pool ecosystems. They often rest on the bottom in shallow water, but also may be found at different layers in the water column in deeper water. The young salamanders are wary; when approached by potential predators, they will dart into vegetation on the bottom of the pool (Storer 1925).

The larval stage of the California tiger salamander usually lasts 3 to 6 months, because most seasonal ponds and pools dry up during the summer (Petranksa 1998). Amphibian larvae must grow to a critical minimum body size before they can metamorphose (change into a different physical form) to the terrestrial stage (Wilbur and Collins 1973). Individuals collected near Stockton in the Central Valley during April varied from 47 to 58 mm (1.85 to 2.3 in) in length (Storer 1925). Feaver (1971) found that larvae metamorphosed and left the breeding pools 60 to 94 days after the eggs had been laid, with larvae developing faster in smaller, more rapidly drying pools. The longer the ponding duration, the larger the larvae and metamorphosed juveniles are able to grow, and the more likely they are to survive and reproduce (Semlitsch *et al.*

1988; Pechmann *et al.* 1989; Morey 1998; Trenham 1998b). The larvae perish if a site dries before they complete metamorphosis (P. Anderson 1968; Feaver 1971). Pechmann *et al.* (1989) found a strong positive correlation between ponding duration and total number of metamorphosing juveniles in 5 salamander species. In Madera County, Feaver (1971) found that only 11 of 30 pools sampled supported larval California tiger salamanders, and 5 of these dried before metamorphosis could occur. Therefore, out of the original 30 pools, only 6 (20 percent) provided suitable conditions for successful reproduction that year. Size at metamorphosis is positively correlated with stored body fat and survival of juvenile amphibians, and negatively correlated with age at first reproduction (Semlitsch *et al.* 1988; Scott 1994; Morey 1998).

The metamorphosed juveniles leave their ponds in the late spring or early summer. Before the pools dry completely, they settle in small mammal burrows, to which they return at the end of nightly movements (Zeiner *et al.* 1988; Shaffer *et al.* 1993; Loredó *et al.* 1996). Like the adults, juveniles may emerge from these retreats to feed during nights of high relative humidity (Storer 1925; Shaffer *et al.* 1993) before settling in their selected upland sites for the dry, hot summer months. Juveniles have been observed to migrate up to 1.6 km (1 mi) from breeding pools to upland areas (Austin and Shaffer 1992).

An estimated 83 percent of the salamanders rely on rodent burrows for shelter (Petranksa 1998). Mortality of juveniles during their first summer exceeds 50 percent (Trenham 1998b). Emergence from upland estivation sites in hot, dry weather occasionally results in mass mortality of juveniles (Holland *et al.* 1990). Juveniles do not typically return to the breeding pools until they reach sexual maturity, at several years of age (Trenham 1998b; Hunt 1998). Trenham (1998b) estimated survival from metamorphosis to maturity at his study site to be less than 5 percent (well below an estimated replacement level of 18 percent). Adult survivorship varies greatly between years, but is a crucial determinant of whether a population is a source or sink (*i.e.*, whether net productivity exceeds the level necessary to maintain the population or it does not).

Lifetime reproductive success for California and other tiger salamanders is low. Trenham *et al.* (2000) found the average female bred 1.4 times and produced 8.5 young that survived to metamorphosis per reproductive effort. This resulted in roughly 11