

of gophers (D. Cook, The Wildlife Society, pers. comm., 2002). Active gopher burrows probably are needed to sustain California tiger salamanders because inactive burrow systems become progressively unsuitable over time. California tiger salamanders cannot persist without estivation habitat.

Adult California tiger salamanders may migrate up to 2 km (1 mi) from their estivation 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 estivation sites and breeding pools depends on local topography and vegetation, and the distribution of ground squirrel or other rodent burrows (Stebbins 1989; Lawrence Hunt, consultant, *in litt.*, 1998). Males migrate 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 intervening habitat (*e.g.*, salamanders may move more quickly through sparsely covered and more open grassland than densely vegetated lands) (Trenham 1998a). As with migration distances, the number of ponds used by an individual over its lifetime will be dependent 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; Petranks 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, they may be attached 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 can not breed (Barry and Shaffer 1994).

Salamander eggs hatch in 10 to 14 days with newly hatched salamanders (larvae) ranging from 11.5 to 14.2 mm (0.45 to 0.55 in) in total length (Petranks 1998). The larvae are aquatic. They are yellowish gray in color and have broad fat heads, possess large, feathery external gills, and broad dorsal fins that extend well onto their 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 and when approached by potential predators 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, as most seasonal ponds and pools dry up during the summer (Petranks 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 (Pechmann *et al.* 1989; Semlitsch *et al.* 1988; Morey 1998; Trenham 1998b). The larvae will 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 five salamander species. In Madera County, Feaver (1971) found that only 11 of 30 pools sampled supported larval California tiger salamanders, and five of these dried before metamorphosis could occur. Therefore, out of the original 30 pools, only six (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).

When the metamorphosed juveniles leave their ponds in the late spring or early summer, before the ponds dry completely, they settle in small mammal burrows at the end of their 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 estivation sites for the dry, hot summer months. Juveniles have been observed to migrate up to 1.6 km (1 mi) from breeding ponds to estivation areas (Austin and Shaffer 1992).

An estimated 83 percent of the salamanders rely on rodent burrows for shelter (Petranks 1998). Mortality of juveniles during their first summer exceeds 50 percent (Trenham 1998b). Emergence from estivation 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; L. Hunt, *in litt.*, 1998). Trenham (1998b) estimated survival from metamorphosis to maturity at his study site at less than 5 percent, well below the estimated replacement level of 18 percent that would maintain the population. 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).

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 metamorphic offspring over the lifetime of a female. Preliminary data suggest that most individuals of the California tiger salamanders require 2 years to become sexually mature, but some individuals may be slower to mature (Shaffer *et al.* 1993). Some animals do not breed until they are 4 to 6 years old. While individuals may survive for more than 10 years, many breed only once, and in some populations, less than 5 percent of marked juveniles survive to become breeding adults (Trenham 1998b). With such low recruitment, isolated populations can decline greatly from unusual, randomly occurring natural events as well as from human caused factors that reduce breeding success and individual survival. Factors