

day or at night, or during a rainfall (Twitty, 1966). Stomach content analysis of terrestrial and aquatic adults revealed that the diet consists of terrestrial organisms only, predominantly insects. Adults apparently do not feed during their aquatic phase, though they will resume feeding if forced back onto land by winter floods (Packer, 1961). Aquatic adults maintained in the lab also do not feed (Licht and Brown, 1967).

O. Predators. No predators have been specifically reported for red-bellied newts. However, Twitty (1966) reported that at his field station in Sonoma County, garter snakes "brazenly stole" newts from storage containers as he and his assistants looked on. Both red-bellied and rough-skinned newts occurred at the field station, but most of Twitty's work there was on red-bellied newts, so presumably this is the species to which he was referring. He did not identify the garter snakes to species, but most likely they were common garter snakes (*Thamnophis sirtalis*), which are known to feed on rough-skinned newts (see rough-skinned newt species account for references).

P. Anti-Predator Mechanisms. The anti-predator mechanisms of red-bellied newts are similar to those described for rough-skinned newts: toxicity, aposematic coloration, and defensive posturing. Ovarian eggs and embryos of red-bellied newts contain high levels of tetrodotoxin (Mosher et al., 1964); all three species of *Taricha* show similar levels of toxicity in this regard (Twitty, 1937; Brodie et al., 1974b). The skin of adult red-bellied newts also contains tetrodotoxin. The toxicity of the back skin of adult female red-bellied newts is similar to that of California newts, but adult rough-skinned newts are considerably more toxic. Brodie et al. (1974b) estimated that 1,200–2,500 mice could be killed by the skin of red-bellied newts (as compared to approximately 25,000 mice for rough-skinned newts). Ovarian eggs and adult skin of red-bellied newts have similar toxicity levels. These high levels of tetrodotoxin render newts inedible to nearly all predators (Brodie, 1977). Animals are dark-colored dorsally and bright tomato-red ventrally. The dark dorsum is cryptic against the forest floor. The defensive posture exposes the aposematic coloration of the ventral surface. During the unken reflex, the tail and head are elevated vertically, revealing the bright red underside of the chin and tail; at the same time, toxic skin secretions are released. The defensive display varies somewhat depending on the state of the salamander or with the intensity of stimulation: the low intensity response is a U-shaped posture involving a vertical elevation of head and tail such that both point skyward. With a high intensity response, the head tips further back and the pelvis and hindlimbs are lifted off the substrate such that the

tip of the snout and the base of the tail almost come into contact. The unken reflex display is generally similar in all species of *Taricha*, but red-bellied newts show one striking variation in posture. Instead of elevating the tail, sometimes the pelvis and hindlimbs remain in contact with the ground, while the head, forelimbs, and body are together lifted from the substrate; this variation in posture may be a result of the longer tail of red-bellied newts counterbalancing the body (Brodie, 1977).

Q. Diseases. None reported.

R. Parasites. None reported.

4. Conservation.

The conservation status of red-bellied newts is uncertain, because no ecological studies have been conducted on this species for the last 35 yr or so. However, this species has a limited and somewhat spotty geographic distribution, and human population pressure has intensified considerably over much of its range. Specifically, conversion of native forests and grasslands to vineyards and subdivisions likely poses a serious threat to red-bellied newts. For example, this change in land use has led to the large-scale removal of trees, resulting in the alteration of temperature, sediment load, and physical structure of rivers and streams, such that they are less hospitable to native anadromous salmonid fishes (Giusti and Merenlender, 2002). It is likely that this degradation of aquatic habitat has also negatively impacted aquatic-breeding salamanders, such as red-bellied newts. Removal of trees also affects the microclimate of terrestrial habitats, perhaps rendering them less suitable for terrestrial newts. Finally, increased vehicular traffic associated with housing subdivisions undoubtedly has resulted in increased mortality of terrestrial newts.

Taricha torosa Rathke, 1833
CALIFORNIA NEWT

Shawn R. Kuchta

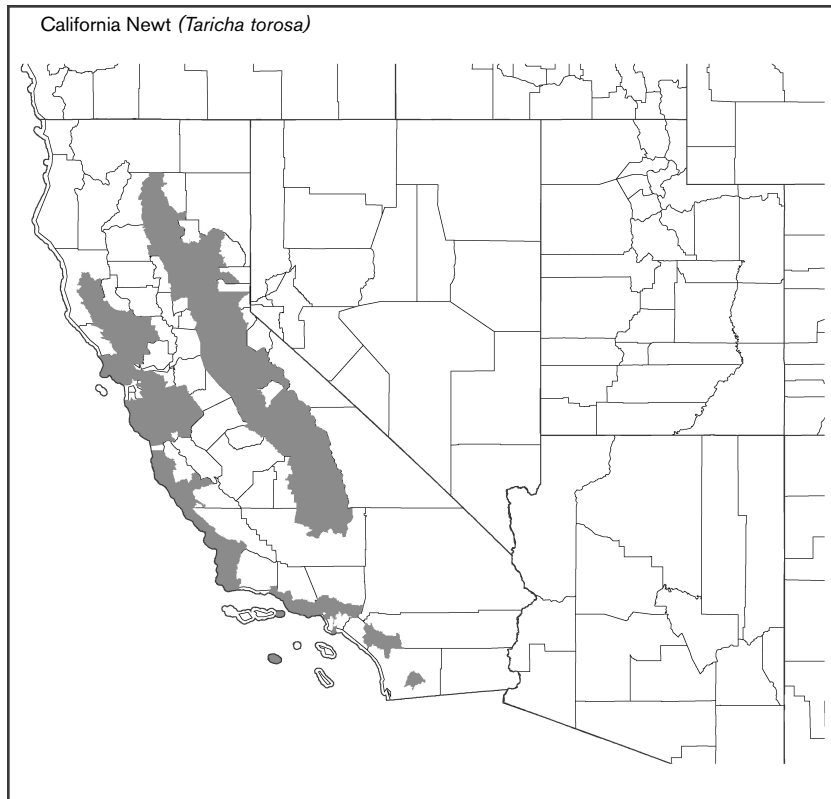
1. Historical versus Current Distribution.

Riemer (1958) conducted the first comprehensive investigation of the distribution and systematics of the genus *Taricha* and recognized 2 allopatric subspecies of *T. torosa* (California newts; Riemer, 1958): *T. t. torosa* (Coast Range newts) and *T. t. sierrae* (Sierra newts). Coast Range newts are distributed from central Mendocino County in northwestern California south through the Coast Ranges to Boulder Creek on the western slope of the peninsular ranges in San Diego County (Stebbins, 1985). Coast Range newts are found from sea level to at least 1,280 m on Mt. Hamilton, Santa Clara County, California (Stebbins, 1959). The southernmost localities in San Diego County compose a

geographic isolate (Stebbins, 1985; Jennings and Hayes, 1994a), and were once recognized as a distinct subspecies (*T. t. klauberi*: Wolterstorff, 1935; Stejneger and Barbour, 1943) or species (*T. klauberi*: Bishop, 1943; Smith and Taylor, 1948). They are genetically distinct (Tan, 1993; Tan and Wake, 1995; Kuchta, 2002) and distinguishable based on morphometric (Riemer, 1958) and osteological (Herre, 1939; Tan, 1993) grounds. However, the initial description was based on pathological animals, and *T. klauberi* was synonymized with *T. torosa* (Myers, 1942b; Twitty, 1942; Stebbins, 1951; Brattstrom and Warren, 1953; see "Parasites" below). Specimens have been reported from northwestern Baja California (Slevin, 1928; Smith and Taylor, 1948), but these records require verification.

Sierra newts occur at elevations below about 2,000 m and range along the western slopes of the Sierra Nevada from Shasta County (Gorman, 1951) south to Kern County (Stebbins, 1985). Many sources report a gap in the distribution between southern Shasta and northern Butte counties, but this may not exist, as Tan (1993) collected specimens in this area (also D. B. Wake, personal communication). Some sources consider Sierra newts to be deserving of specific status (Twitty, 1942; Collins, 1991; Tan, 1993; Kuchta, 2002), but others disagree (Stebbins, 1951; Riemer, 1958; Frost et al., 1992; Montanucci, 1992; Van Devender et al., 1992).

Tan and Wake (1995) outlined the historical biogeography of California newts. Based primarily on mitochondrial DNA evidence, they propose that Coast Range newts and Sierra newts differentiated about 8 million yr ago (mya), when Sierra newts existed in the uplifting central Sierra Nevada, and Coast Range newts inhabited the present day San Diego area. Roughly 5 mya, Coast Range newts expanded their distribution north to Monterey, while Sierra newts spread north and south in the Sierra Nevada. Coastal populations of Coast Range newts invaded the southern Sierra Nevada and differentiated morphologically roughly 2 mya; Tan (1993) and Kuchta (2002) suggest these populations are sufficiently divergent to warrant species status. Only relatively recently, after the central California inland sea subsided, did Coast Range newts expand north of Monterey to their current distribution. Early workers have suggested, based on differences in larval pigmentation (Twitty, 1942) and preliminary genetic data (Coates, 1967; Hedgecock and Ayala, 1974; Hedgecock, 1976), that Coast Range newts are further divisible into northern and southern "races" located on either side of the Salinas Valley in Monterey County. While a genetic break exists, it is not large relative to other genetic disjunctions in the species (Tan, 1993; Kuchta, 2002).



2. Historical versus Current Abundance.

Historically, California newts were abundant throughout much of their range, except in the Santa Ynez Mountains of Santa Barbara County, where populations may have always been small (S. Sweet, personal communication, reported in Jennings and Hayes, 1994a). In southern California, suitable habitat is patchy (Jennings and Hayes, 1994a); however, at appropriate sites California newts were historically "common" on the Pacific slope (Klauber, 1928, 1930; Bogert, 1930; Pequegnat, 1945; Dixon, 1967; Brattstrom, 1988).

3. Life History Features.

Some of the best documentation of California newt life history features is by Ritter (1897) and Storer (1925), both of whom worked in the northern part of the range. Unfortunately, both California newts and rough-skinned newts (*T. granulosa*) occur there, and rough-skinned newts were not recognized as a distinct species until the work of Twitty (1935). However, California newts are the more abundant species in this area, and below I cite these authors where I feel the information applies to California newts.

A. Breeding.

i. Breeding migrations. Coast Range newts migrate to ponds from December-early May, depending on locality, weather conditions, and breeding habitat. Miller and Robbins (1954) state that the migration of Coast Range newts to breeding ponds requires 6-8 wk, but this has not

been rigorously studied. Mating at any one site lasts from 3-12 wk (Miller and Robbins, 1954; De Lisle et al., 1986; Gamradt et al., 1997), and in all situations males arrive before females and remain at the breeding site longer (Ritter, 1897; Smith, 1941; Stebbins, 1951; Miller and Robbins, 1954; Riemer, 1958). In the vicinity of Palo Alto and Berkeley, migrations of pond breeding populations occur from late December to early February (Storer, 1925; Twitty, 1942; Stebbins, 1951; Miller and Robbins, 1954; Riemer, 1958). However, in the same area, stream breeding populations migrate in March and April after spring flooding subsides (Storer, 1925; Twitty, 1942; Stebbins, 1951; Miller and Robbins, 1954; Riemer, 1958). Southern Coast Range newts also migrate in March and April (Storer, 1925; Brame, 1968; Kats et al., 1992), probably because they too breed most commonly in streams. Sierra newts migrate to breeding sites in January and February, and breed from March to early May (Stebbins, 1951; Riemer, 1958).

Brown (S. C.) and P.S. Brown (1980) investigated water balance in California newts and suggest that they possess some features analogous to terrestrial anurans, such as toads in the family Bufonidae. They discovered that the urinary bladder could store fluids in excess of 50% of the total body weight, and that water could be resorbed from the bladder. They also found that water is pulled from the ventral to the dorsal surface of the body,

probably via capillary action acting on the warty skin of terrestrial individuals (see also Lillywhite and Licht, 1974).

ii. Breeding habitat. Coast Range newts breed in ponds, reservoirs, and streams (Storer, 1925; Twitty, 1942; Riemer, 1958). Gamradt and Kats (1997) document that stream-breeding newts in southern California commonly lay eggs in deep, slow pools, occasionally in runs, and almost never in riffles. Egg masses are attached to aquatic vegetation, branches, and the outer surfaces of rocks (Ritter, 1897; Storer, 1925; Twitty, 1942). In the central and northern portions of their range, Coast Range newt egg masses are not laid under rocks (Twitty, 1942); but in southern California, egg masses are commonly laid under rocks in quiet stream pools (Gamradt and Kats, 1996, 1997).

Sierra newts are more stream adapted than Coast Range newts. Relative to Coast Range newts, and analogous to the stream-breeding red-bellied newts (*T. rivularis*), breeding Sierra newt males possess a reduced tail fin, and females lay eggs that are larger and commonly placed on the undersides of rocks in running water (Twitty, 1942). Sierra newts will, however, breed in ditches and other bodies of water with little or no current (Twitty, 1942).

B. Eggs.

i. Egg deposition sites. Storer (1925) observed that eggs are most frequently found from 7.5-10 cm deep, and when water levels rise to 30 cm or more the eggs die. Mosher et al. (1964) reports finding eggs from a few centimeters to >1.5 m deep.

ii. Clutch size. California newts lay eggs in masses ranging from about 7-47 eggs (Ritter, 1897; Storer, 1925; Twitty, 1942; Brame, 1956, 1968; Mosher et al., 1964). Data are sparse, but it seems females lay from 3-6 masses each (Ritter, 1897; Brame, 1968). Miller and Robbins (1954) report for a sample of newts from central coastal California that the average Coast Range newt ovary contains 130-160 ova.

C. Larvae/Metamorphosis.

i. Length of larval stage. The larval stage lasts several months, with metamorphic animals leaving the water in summer or fall, depending on conditions. Ritter (1897) observed that the average larval period runs from March-October near Berkeley, California. He estimated the average size at metamorphosis to be 47 mm TL. Bishop (1943) noted that metamorphosis for Coast Range newts begins in early September and continues for some months; he estimates average size at metamorphosis at 50 mm TL, with large individuals measuring 60 mm. Twitty (1935) estimates the size at metamorphosis as approximately 45-55 mm TL. In 1998, at a vernal pool in Sonoma County, I found the average size of 13

metamorphic animals to be 43.8 ± 2.0 mm TL (24.6 ± 1.2 mm SVL). The average weight of 14 metamorphic animals was 0.45 ± 0.1 g. Metamorphosis began on 22 July and ended on 3 August, after the pool dried completely. Metamorphosis in Sierra newts does not seem to have been monitored. Bishop (1943) notes that larvae collected in late August range from 55–62 mm TL.

Kaplan (1985) examined the effects of egg size and food availability on larval development. Larvae from large eggs, when given an abundance of food, grew bigger and metamorphosed sooner than larvae from small eggs. Average time to metamorphosis from the feeding stage ranged from about 75–92 d; size ranged from 23.5–27 mm SVL. Conversely, under food stress, larvae from large eggs, though still metamorphosing at a larger size, took much longer to reach metamorphosis than larvae from small eggs. Average time to metamorphosis from the feeding stage ranged from roughly 105–190 d; size at metamorphosis was 21–23.75 mm SVL. This study suggests, among other things, that larger eggs may not be advantageous when food is limited and there is the threat of habitat desiccation.

Riemer (1958) suggests that only rough-skinned newts are known to overwinter as larvae, yet Storer (1925) collected four California newt larvae in Bailey Canyon, Los Angeles County, in April and May 1909, measuring 52–63 mm that were nearing completion of metamorphosis. Nevertheless, it seems that overwintering by California newt larvae is uncommon.

ii. Larval Requirements.

a. Food. California newt larvae eat small invertebrates, but their diet has not been rigorously studied. Ritter (1897) observed that larvae will eat decomposing organic matter, and perhaps conspecifics. Storer (1925) reports them feeding on mosquito larvae in captivity.

b. Cover. Adult Coast Range newts are cannibalistic (Ritter, 1897; Kats et al., 1992; Hanson et al., 1994; L. Kats, unpublished data, as cited in Elliott et al., 1993). Accordingly, Elliott et al. (1993) showed that lab-reared Coast Range newt larvae (14–17 mm TL) from the Santa Monica Mountains use cover more when provided chemical cues from adult newts. In the same study, chemical cues from odonate naiads and belostomatids (Hemiptera)—both known predators of larvae—did not result in substantially more cover use than controls, although the use of cover increased qualitatively.

In a second study, Kats et al. (1994) found that younger larvae use cover significantly more than older larvae. The behavior does not seem to be size dependent, and the authors suggest that the reduced use of cover is a product of reduced predation, as adult newts typically leave the streams by July.

iii. Larval polymorphisms. Albino larvae have occasionally been found (Riemer, 1958; Wells, 1963; Dyrkacz, 1981).

iv. Features of metamorphosis. Similar to many amphibians, California newt larvae are induced to metamorphose by pond drying (personal observations). At breeding sites with permanent water, the factors influencing metamorphosis remain unstudied. The most detailed description of metamorphosis is by Ritter (1897). The first sign is the development of a dusky color on the dorsum and a tinge of yellow on the venter. Subsequently, the colors deepen rapidly, the tail fin is absorbed from anterior to posterior, and the gills are absorbed. When metamorphic animals leave the water they possess adult coloration (though the larval pigment pattern is visible underneath), the skin is granular, and the gills are reduced to dark stubs. In the lab, this process requires over 2 wk (Ritter, 1897). If newly metamorphosed animals are kept in water, they will drown (Ritter, 1897).

v. Post-metamorphic migrations. California newts leave the aquatic habitat after metamorphosis, and do not return until they breed. Dispersal into the terrestrial landscape—where and how far they travel, the environmental clues employed in dispersal, and the length of the juvenile stage—is in need of study. Trenham (1998) recaptured marked juveniles up to 3,500 m from their natal ponds.

vi. Neoteny. Neoteny is unreported, but in permanent bodies of water California newt adults can remain aquatic year-round, and in this situation males retain their secondary sexual characters (Miller and Robbins, 1954). For example, on land adjacent to the University of California's Hastings Natural History Reserve, in Monterey County, a pond was deepened such that in the summers it no longer dried; the following summer a large population of adults took up permanent residence in the pond (P. Trenham, personal communication).

D. Juvenile Habitat. Unstudied.

E. Adult Habitat. The terrestrial ecology of California newts is incompletely studied, hampering conservation efforts (Jennings and Hayes, 1994a). In central California, Coast Range newts are found in mountainous or rolling woodland and grassland (Riemer, 1958; personal observations). In southern California, Coast Range newts inhabit a drier zone of chaparral, oak woodland, or grassland (Riemer, 1958). Sierra newts are found in mixed Sierran Forest.

F. Home Range Size. Unknown.

G. Territories. Unknown.

H. Aestivation/Avoiding Desiccation. California newts leave the aquatic habitat within a few weeks of breeding, and aestivate terrestrially during the dry summer. Mesic microclimates, such as deep leaf litter and animal burrows, are used as aestivation sites, and some individuals migrate

considerable distances to them (see "Seasonal Migrations" below; Trenham, 1998). Not all aestivation sites are distant from water, however, as Stebbins (1951) reports unearthing 14 aestivating adults 1.5 m from a stream in Los Angeles County. The aestivation site was under a boulder, in a hole partly filled with "slightly damp, coarse sand" (p. 25).

I. Seasonal Migrations. Following metamorphosis, California newts emigrate from the breeding site and spend the next few years growing to sexual maturity (see "Age/Size at Reproductive Maturity" below). When sexually mature, they migrate to a breeding site during winter or spring rains to mate (see "Breeding migrations" above). Following mating, they typically return to the terrestrial environment. Miller and Robbins (1954) found that about half of males and females of breeding size had immature gonads. If California newt breeding resembles red-bellied newt breeding, males typically breed annually while females skip 1, 2, or more years between reproductive events (Twitty, 1966).

California newts can migrate large distances between breeding and aestivation sites. For example, Trenham (1998) recaptured adult newts up to 3,200 m from the breeding pond where they were marked. However, when suitable aestivation sites are nearer, migrations may not be so long (P. Trenham, personal communication; see "Aestivation/Avoiding Desiccation" above). California newts typically return to the same breeding site repeatedly (but see Trenham, 1998). Endler (1970) demonstrated experimentally that California newts exhibit a kinesthetic, or body position, sense in their homing behavior, and observed that migrating newts correct for movements around objects such that a straight course is maintained. Twitty (1966) established the importance of olfaction in the navigation of red-bellied newts, and Landreth and Ferguson (1967a,b) demonstrated the use of celestial cues in the navigation system of rough-skinned newts. None of these experiments have been replicated on California newts.

J. Torpor (Hibernation). Not known to exist.

K. Interspecific Associations/Exclusions. Aside from the recent work of L. Kats and colleagues, little is known about the community ecology of California newts (see "Conservation" below for a discussion of introduced predators). In southern California and the Sierra Nevada, California newts are the only stream-breeding salamander.

L. Age/Size at Reproductive Maturity. Riemer (1958) found the smallest sexually mature animals to be around 50 mm, but there is variation. Both Ritter (1897) and McCurdy (1931) estimate the age of reproductive maturity to be reached after 3 yr; however, neither followed marked animals

in the field. Work on experimentally released *rivularis-torosa* and *rivularis-sierrae* hybrids suggests that reproductive maturity requires 7–8 yr or longer (Twitty, 1961b, 1966). Unfortunately, these recapture data were never clearly summarized before Twitty's untimely death, and it is unclear how relevant hybrid data are to California newt sexual maturity.

M. Longevity. The longevity of California newts is unknown, although the animals are certainly long-lived. If red-bellied newts are any indication (Twitty, 1966), many California newts live to be > 20 yr old.

N. Feeding Behavior. Adult California newts feed terrestrially with a highly developed tongue-projection system, including substantial anterior movement of the ceratohyal (Findeis and Bemis, 1990). Conversely, aquatic feeding by adults is gape-and-suck, and further specialization of the feeding apparatus is probably constrained by trade-offs imposed by feeding both terrestrially and aquatically (Findeis and Bemis, 1990).

There has been no systematic study of the diet of terrestrial California newts, but Ritter (1897) reports that newts feed on their own sloughed-off skin, earthworms, insect adults and larvae, sowbugs, small snails and slugs, and other small invertebrates. Adults in the aquatic environment have been observed to feed on coleopterans, lepidopterans, and plecopterans (Hanson et al., 1994), ephemeropterans and the oligochaete *Eisenia rosea* (Kerby and Kats, 1998), and probably on the egg masses of California red-legged frogs (*Rana draytonii*; Rathbun, 1998; newts not identified to species). Furthermore, several workers have documented predation by adults on conspecific egg masses, both during and after oviposition (Ritter, 1897; Pequegnat, 1945; Kaplan and Sherman, 1980; Marshall et al., 1990; Kats et al., 1992), and on conspecific larvae (Ritter, 1897; Kats et al., 1992; L. Kats, unpublished data, as cited in Elliott et al., 1993, and Kats et al., 1994; Hanson et al., 1994). Hanson et al. (1994) found a nestling bird (0.3 g), probably Anna's hummingbird (*Calypte anna*), in the stomach of a small female newt in southern California.

O. Predators. The egg masses, embryos, and adults of California newts possess tetrodotoxin (TTX), a potent neurotoxin, and are thus generally unpalatable (see "Anti-Predator Mechanisms" below). Only common garter snakes (*Thamnophis sirtalis*) have been systematically shown to possess resistance to TTX (Brodie and Brodie, 1970). However, California newt larvae are not poisonous (see "Anti-Predator Mechanisms" below), and individuals in this life history stage may be an important food resource for newborn individuals of some garter snakes (Fitch, 1940, 1941; Fox, 1951), including Federally Endangered San Francisco garter

snakes (*T. s. infernalis*; S. Barry, personal communication, as cited by Jennings and Hayes, 1994a). I examined the stomach contents of 23 live Pacific Coast aquatic garter snakes (*T. atratus*) in Sonoma County, California, and found five with one or more California newt larvae in their stomach. Fox (1951) reports finding California newt adults in the stomach of Pacific Coast aquatic garter snakes. Jennings and Cook (1998) found that introduced American bullfrogs (*Rana catesbeiana*) in Sonoma and Riverside counties not only eat larval California newts, but surprisingly also adults. Kats et al. (1998), in Los Angeles County, discovered a ring-necked snake (*Diadophis punctatus*) eating an adult newt, but the snake was lethargic, and in the lab regurgitated the dead newt. Also in southern California, two introduced predators, crayfish and mosquitofish, are causing serious declines (see "Conservation" below) via predation on egg masses and larvae. For a discussion of cannibalism of egg masses, see "Feeding Behavior" above.

P. Anti-Predator Mechanisms. Adults and embryos of California newts contain the potent neurotoxin TTX (Twitty and Johnson, 1934; Twitty, 1937; Wakely et al., 1966; Brodie et al., 1974b). This is the same toxin as found in the ovaries of puffer fish (family Tetraodontidae; Buchwald et al., 1964), as well as in a variety of other taxa, including other amphibians (Daly et al., 1987), echinoderms (Maruyama et al., 1984), cephalopods (Sheumack et al., 1978), and bacteria (Noguchi et al., 1986; Thuesen and Kogure, 1989). It is possible that this neurotoxin is produced by symbiotic gut bacteria (Mosher and Fuhrman, 1984; Noguchi et al., 1986, 1987; Thuesen and Kogure, 1989), but the situation is complex and it is not clear how newts acquire TTX (Mosher and Fuhrman, 1984; Daly et al., 1987). TTX is found in the skin, ovaries and ova, muscle, and blood of adult newts; the liver, viscera, and testes contain only minute amounts (Wakely et al., 1966). Embryos possess TTX throughout their body, but larvae lose their toxicity shortly after the yolk is absorbed (Twitty and Johnson, 1934; Twitty, 1937), suggesting that embryos obtain their poison maternally.

Rough-skinned newts are the most toxic salamanders in the world, and California newts are reported to be about 1/10 as toxic (Brodie et al., 1974b). To put this in perspective, Brodie et al. (1974b) estimated that the skin of adult rough-skinned newts from Benton County, Oregon, could potentially kill 25,000 20-g mice, whereas the skin of adult California newts could kill 1,200–2,500 20-g mice. More recent work has uncovered substantial geographic variation in the toxicity of rough-skinned newts (Hanifin et al., 1999). Variation in California newt toxicity is in need of examination.

California newts have a cryptic brown dorsum and an aposematic yellow-to-orange venter. When harassed, California newts assume a defensive posture called the *unken reflex*, which exposes the ventral aposematic coloration: the belly is pressed down against the substrate, the throat raised up with eyes closed and depressed, the limbs stiffly extended outward, and the tail raised straight over the body (Stebbins, 1951; Riemer, 1958; Johnson and Brodie, 1972, 1975; Brodie, 1975; rough-skinned newts curl their tail tip; Riemer, 1958). Toxicity, aposematic coloration, and defensive posturing form a co-adaptive unit (Johnson and Brodie, 1972, 1975; Brodie, 1977). Naylor (1978) has suggested that the frontosquamosal arch of newts is an anti-predator adaptation designed to add structural support to the skull and protect retracted eyes. California newts produce a repertoire of sounds (Davis and Brattstrom, 1975), and Brodie (1978) suggests that predators may associate some sounds with toxic skin secretions.

Q. Diseases. Unknown. Some animals in San Diego County exhibit extreme wartiness now recognized as pathological (see "Historical versus Current Distribution," above and "Parasites," below).

R. Parasites. Ingles (1936), Lehmann (1954), and Goldberg et al. (1998c) documented the presence of parasites in California newts. Goldberg et al. (1998c) found that in 68 Coast Range newts from Orange and Los Angeles counties, 52 were infected with at least one nematode. Four nematode species were discovered (average number of nematode species/infected newt = 1.3 ± 0.5), and they concluded that the parasite infracommunities of California newts are depauperate relative to other vertebrates. There are no data on the effect of parasite loads on the fitness or ecology of California newts. Some animals in San Diego County exhibiting extreme wartiness were once recognized as a distinct taxon, but it was later determined that the warty phenotype was pathological (see "Historical versus Current Distribution" above).

4. Conservation.

California newt populations are impacted by breeding site degradation (Jennings and Hayes, 1994a), destruction of summer aestivation sites and migration routes (Jennings and Hayes, 1994a; see also Semlitsch, 1998), road kills (Storer, 1925; R. C. Stebbins, personal communication; P. Trenham, personal communication), large-scale commercial exploitation (Jennings and Hayes, 1994a), altered sedimentation dynamics in stream pools resulting from wildfires (Gamradt and Kats, 1997; Kerby and Kats, 1998), and riparian habitat degradation (Faber et al., 1989; Jennings and Hayes, 1994a).

Furthermore, in the Santa Monica Mountains of Los Angeles County, two

introduced predators, crayfish (*Procambarus clarkii*) and mosquitofish (*Gambusia affinis*), have caused serious declines and exterminated some populations (Gamradt and Kats, 1996; Gamradt et al., 1997). Crayfish are sold as bait, and mosquitofish are distributed broadly for mosquito control, so both are widespread (Gamradt and Kats, 1996). Also in the Santa Monica Mountains, Anzalone et al. (1998) showed that solar UV-B causes high rates of embryonic mortality in California newt egg masses (see also Blaustein et al., 1998). The genetically distinct San Diego County populations in the Cuyamaca Mountains (see "Historical versus Current Distribution" above) are currently restricted to the Boulder, Ceder, and Conejos Creek systems, where populations persist in small, isolated pockets (from about 15–20 breeding adults; E. Ervin, USGS, personal communication). Exotic predators such as crayfish, green sunfish (*Lepomis cyanellus*), and rainbow trout (*Oncorhynchus mykiss*) occur in the perennial reaches of streams originating in the Cuyamaca Mountains of San Diego County. Because these predators and California newts do not co-occur, they may be excluding newts (E. Ervin, USGS, personal communication). Finally, Fisher and Shaffer (1996) document a decline of California newts in the central valley of California, where these animals are peripherally present.

California newt populations south of the Salinas River in Monterey County are considered by the California Department of Fish and Game to be Species of Special Concern (Jennings and Hayes, 1994a). While this designation carries no legal weight, it is a helpful management tool highlighting concerns about the species' status. Moreover, a large portion of verified populations in San Diego County are extinct (Jennings and Hayes, 1994a), and because of the distinctiveness of the animals in this area (see "Historical versus Current Distribution" above) the status of these populations warrants further investigation.

Family Sirenidae

Pseudobranchius axanthus Netting and Goin, 1942(b)

SOUTHERN DWARF SIREN

Paul E. Moler

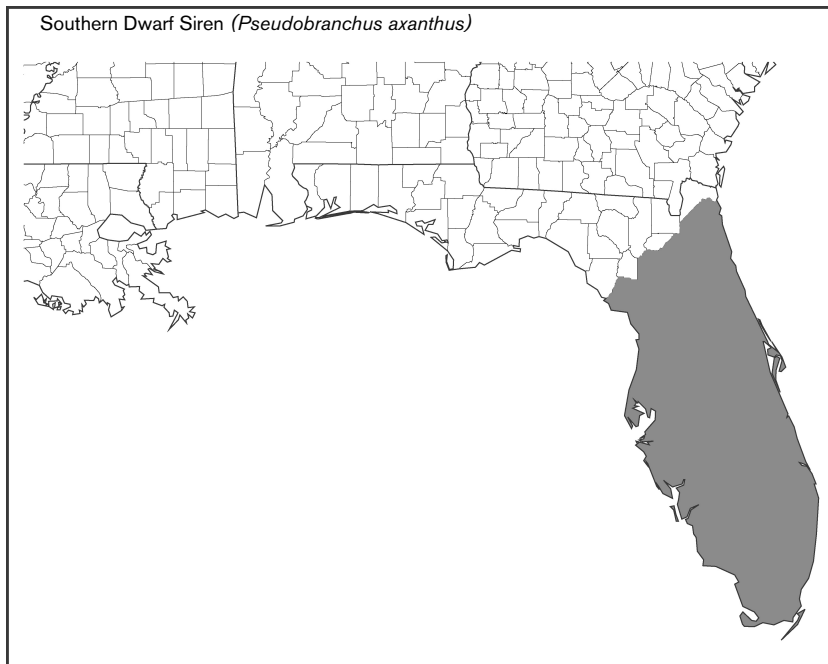
1. Historical versus Current Distribution.

Southern dwarf sirens (*Pseudobranchius axanthus*) are restricted to peninsular Florida; their northern boundary includes Alachua, Clay, Duval, Levy, and Putnam counties. Two subspecies, narrow-striped dwarf sirens (*P. a. axanthus*) and Everglades dwarf sirens (*P. a. belli*), are recognized (Moler and Kezer, 1993; Crother et al., 2000). The current distribution of southern dwarf sirens is undoubtedly reduced compared

with their historical distribution, as wetlands in peninsular Florida have been reduced through drainage of surface waters associated with residential, agricultural, and silvicultural development.

D. Juvenile Habitat. Same as adult habitat.

E. Adult Habitat. Southern dwarf sirens are most abundant in heavily vegetated marshes and shallow lakes (Carr, 1940a).



2. Historical versus Current Abundance.

Southern dwarf sirens are often common in suitable habitat. Current numbers are reduced relative to historical abundance due to the loss of wetland habitat.

3. Life History Features.

A. Breeding. Reproduction is aquatic.

i. Breeding migrations. Southern dwarf sirens do not migrate. They breed and permanently reside in the same aquatic habitats.

ii. Breeding habitat. Southern dwarf sirens live and breed in heavily vegetated marshes and shallow lakes.

B. Eggs.

i. Egg deposition sites. Eggs are laid singly or in small bunches among aquatic vegetation throughout the spring (Carr, 1940a; Netting and Goin, 1942b). According to Petranka (1998) the oviposition period lasts from early November to March. Newly laid eggs average 3 mm and are surrounded by the vitelline membrane and three jelly envelopes (Noble and Richards, 1932; see also Petranka, 1998).

ii. Clutch size. Unknown.

C. Larvae. Newly hatched larvae are between 10–11.5 mm SVL, colored brown dorsally with lighter stripes on the dorsal midline and lateral portions of the body and head (Goin, 1947c; see also Petranka, 1998). They have limb buds (Noble, 1927b). Ashton and Ashton (1988) indicate *Pseudobranchius* larvae make take 2 yr to reach sexual maturity.

They may be abundant in floating mats of vegetation or in mucky shoreline deposits.

F. Home Range Size. Unknown.

G. Territories. Unknown.

H. Aestivation/Avoiding Desiccation.

Southern dwarf sirens burrow into bottom sediments and form a protective cocoon when wetlands dry. Individuals may remain buried for several months until their wetland refills (Freeman, 1958; Etheridge, 1990a).

I. Seasonal Migrations. None.

J. Torpor (Hibernation). Carr (1940a) reported that southern dwarf sirens "have been found hibernating in deep mud." Nevertheless, although they may become inactive during prolonged periods of cold weather, they may be collected throughout the winter, especially in southern Florida.

K. Interspecific Associations/Exclusions. Southern dwarf sirens occur sympatrically, but only occasionally syntopically, with northern dwarf sirens (*P. striatus*) in northern peninsular Florida. In areas of sympatry, northern dwarf sirens are typically found in more acidic habitats than are southern dwarf sirens, but they are known to occur syntopically at a few sites (Moler and Kezer, 1993).

L. Age/Size at Reproductive Maturity. Unknown.

M. Longevity. Unknown.

N. Feeding Behavior. Reported foods include amphipods, chironomid larvae, aquatic oligochaetes, and ostracods