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The Status of the California Tiger Salamander (*Ambystoma californiense*) at Lagunita: A 50-year Update

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ABSTRACT.—We review the history of the California tiger salamander (*Ambystoma californiense*) population at Lagunita, a 114-year old reservoir at Stanford University, Santa Clara County, California. The animals apparently colonized the reservoir during the late 19th century, reached a population peak during the first half of the 20th century, and have declined since to near extinction. The apparent causes of this decline are habitat loss due to urbanization, adult salamander mortality from automobiles, loss of larvae during the annual reservoir drainage, and possibly predation by transient fish populations. Recommendations to preserve the population and to allow its size to increase include: (1) construction of a drift fence and tunnel system to divert migrating adults and juveniles underneath the highway, (2) maintenance of water levels through mid-summer to allow most larvae to complete metamorphosis, and (3) excavation of sumps in the lake bed to entrap larvae and keep them from being swept down the lake drain.

The California tiger salamander, *Ambystoma californiense*, is endemic to the San Joaquin-Sacramento river valleys, bordering foothills, and coastal valleys of central California. Adult *A. californiense* average about 190 mm in total length, and are black with scattered white or yellow dorsal and lateral spots (adult and larva illustrated by Stebbins, 1985). Larvae are yellowish-grey, and are of the "pond type," distinguished by the presence of long, feathery external gills and an elongated dorsal-caudal fin (Stebbins, 1951). In this report we summarize the life history of this declining amphibian, detail the decline and rediscovery of the well-known Stanford University Lagunita population, and discuss the water and land management practices over the past 100 years at Lagunita. We focus on Lagunita as an example of a highly managed population of vernal pool amphibians, and discuss how such populations can be maintained under severely impacted ecological conditions.

LIFE HISTORY

Ambystoma californiense is widely-distributed in the relatively xeric central California valleys and foothills, an area characterized by cool, rainy winters and hot, dry summers. This region was originally composed of several million hectares of perennial grasslands intermixed with annual grasses, forbes, and open oak woodlands (Sims, 1988). Today, it has been reduced to remnant grasslands composed of introduced annual species primarily in the low hills that flank the major river valleys (Heady, 1977). Metamorphosed salamanders aestivate for the summer and autumn in burrows of California ground squirrels (*Spermophilus beecheyi*) or valley pocket gophers (*Thomomys bottae*), and emerge only after autumn rains commence, usually by early November (Storer, 1925). Adults congregate at breeding sites, which usually are shallow ephemeral pools and ponds that fill during heavy winter rains. Spawning occurs within a few days of migration and the adults apparently leave the ponds at night soon afterward (Storer, 1925). The eggs hatch from two to four weeks after deposition (Storer, 1925; Twitty, 1941). Larvae feed on algae and aquatic invertebrates (Anderson, 1968), grow rapidly, and metamorphose as the pond water level recedes in late spring or summer (Storer, 1925; Holland et al., 1990). During drought years, some ephemeral rain pools do not fill at all and local *A. californiense* populations may not breed (Shaffer, unpubl. data); presumably the longevity of *A. californiense* adults is sufficient to ensure local population survival through all but the longest droughts.

Adult *A. californiense* are rarely encountered, even where they are known to be abundant. Observations during 1992–1993 of a breeding locality at Hastings Natural History Reservation in Monterey County demonstrated a prolonged period of terrestrial activity by juveniles and adults throughout much of the autumn and winter, although mass migrations are limited to a few rainy nights (Shaffer, Koenig, and Stomberg, unpubl. data). Because the salamanders are generally found only on roadways during these mass migrations, even casual observations of adults are quite unlikely, especially during rainy winters. If the sole objective is to locate *A. californiense* populations, it is far more productive to seine likely ponds for larvae during the spring.

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We believe that *A. californiense* will soon be in danger of extinction throughout its range. It is already gravely threatened in the San Francisco Bay Area and in the San Joaquin Valley immediately east of the Bay Area Counties (Shaffer, unpubl. obs.). The primary cause is the conversion of grasslands to urban or agricultural uses in central California. Ephemeral pools and aestivation sites are eliminated during such land development, and grading operations probably destroy large numbers of adult salamanders. As long ago as 1966 R. Stebbins (pers. comm.) suggested *A. californiense* for inclusion on the first federal endangered species list (Bureau of Sport Fisheries and Wildlife, 1966), and the animal was listed as "depleted" in the first edition of the International Union of Nature and Natural Resources (IUCN) Red Data Book (Honegger, 1968). *Ambystoma californiense* is currently listed as "vulnerable" by the IUCN (IUCN, 1990), and is under consideration for listing as endangered by the U.S. Fish and Wildlife Service (Long, 1992). As development continues, it is clear that land and waterway management in relatively urbanized surroundings will be necessary if *A. californiense* is to survive over much of its range.

The Lagunita Population

Only four *A. californiense* populations have been discussed in the literature. Storer (1925) and Anderson (1968) studied the life histories of *A. californiense* populations respectively near Bellota and Friant in the San Joaquin Valley, and Holland et al. (1990) reported observations on a population in interior San Luis Obispo County, near the southwestern edge of the species' range. The fourth population is located at Lagunita Reservoir on the Stanford University Campus, Santa Clara County, in the southeastern San Francisco Peninsula. Storer (1925) and Myers (1930) reported the existence of the Lagunita population, and Twitty (1941) detailed the reproductive biology of these salamanders. This section of the Bay Area is one of California's oldest urban areas, and Lagunita has the longest history of continuing human manipulation of any *A. californiense* locality. It thus represents an excellent model for the potential coexistence of urban development and salamanders.

Lagunita (Fig. 1) was created by construction of a dam in a meadow at the eastern base of the Santa Cruz Mountain foothills in 1878 or 1879. Leland Stanford Sr., a former Governor of California, and proprietor of the farm that in 1891 became Stanford University, impounded the lake to provide irrigation for his vineyards (L. Long, Stanford Archives, pers. comm.). Lagunita was originally a reservoir of about 10 ha, with a capacity of about 400,000 m^3, and an average depth of about 4 m. The dimensions remain roughly the same today but the capacity has been reduced to about 300,000 m^3 (average depth reduced to about three meters) to reduce the risk of flooding (L. Andrews, Stanford Water Dept., pers. comm.). Rainwater that accumulated during the winter was supplemented during the springtime by water imported via a flume from nearby San Francisquito Creek. Governor Stanford apparently decided at the outset to allow Lagunita's waters to recede and disappear annually, so sometime during the spring or early summer water importation from the creek was discontinued. The reason for this is unrecorded, but it is likely that Stanford's "riparian rights" to draw water from the creek were limited because the creek flow recedes substantially during the summer.

Several amphibian species colonized Lagunita. Lagunita specimens of the coast newt (*Taricha torosa*), the western toad (*Bufo boreas*), the Pacific treefrog (*Hyla regilla*), and the red-legged frog (*Rana aurora*) are present in California museums. Myers (1930) reported a large population of newts at Lagunita, but this species has apparently disappeared from the lake, because SJB's surveys during the 1970s and HBS's surveys during the 1990s yielded no specimens of this normally very abundant and ubiquitous salamander. HBS found no red-legged frog larvae or adults at Lagunita, but SJB found it relatively abundant there and at San Francisquito Creek at least until 1978. Our surveys also show that the bullfrog (*Rana catesbeiana*), a non-native ranid that has replaced *Rana aurora* throughout much of the latter's range (Moyle, 1973), has seemingly failed to colonize the lake.

In the meadow that became Lagunita there may have been vernal pools with *A. californiense* populations, or tiger salamanders could have colonized Lagunita from other nearby populations. Twitty (1941) cites two such natural populations within a few km of Lagunita. According to Twitty (1941), a 13 ha hillside southwest of the lake served as the aestivation site for the Lagunita population.

The first Stanford Natural History Museum *A. californiense* were obtained in 1923, and at least 160 Lagunita specimens exist in California museums, many more than from any other locality. In earlier times *A. californiense* was apparently abundant at Lagunita. The best evidence of this was Twitty's (1941) account of two migrations across Mayfield Road (since renamed Junipero Serra Boulevard), which separates Lagunita from the hillside aestivation area southwest of the lake. The migrations were found on the rainy nights of 1 and 3 January 1940, when respectively 45 (during a one-hour search) and 28 animals (during 2.5 hours) were

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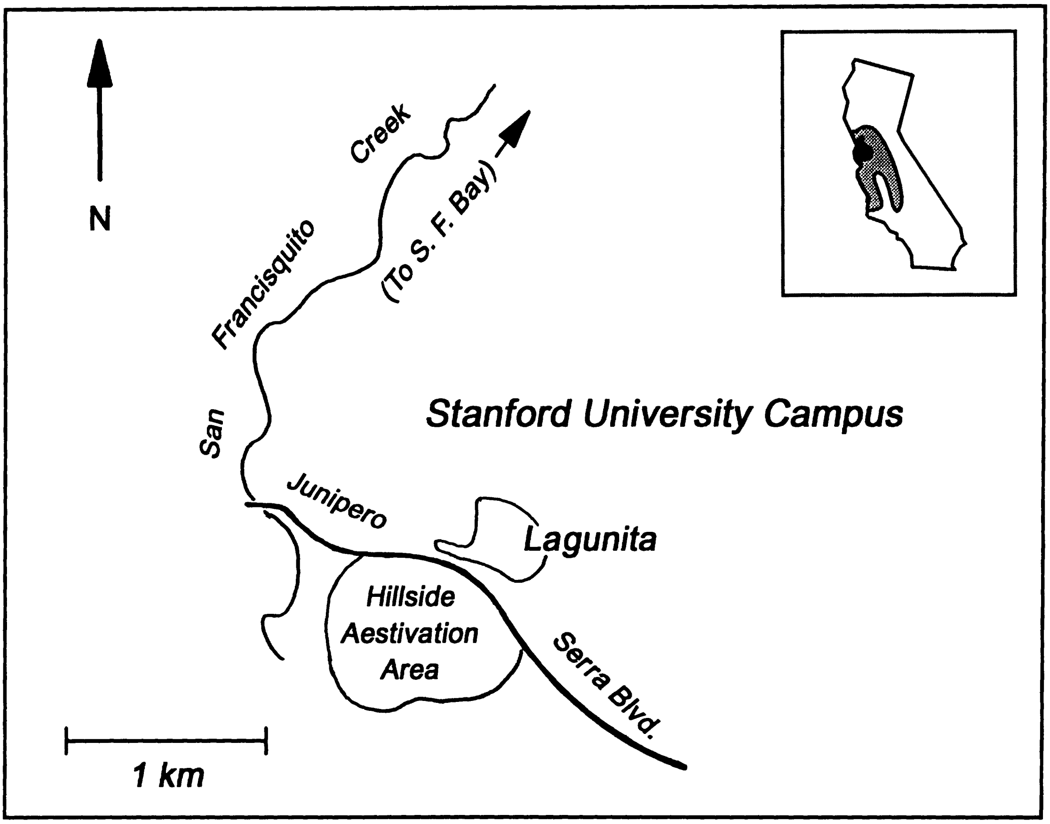

FIG. 1. Map of Lagunita region at Stanford University. Inset California map depicts the approximate distribution of *A. californiense* (shaded region), and the dot denotes Lagunita.

found. Twenty-eight of the first group were road kills, as were at least five of the second. According to old maps, this road was a major Peninsula thoroughfare during that era, so the high mortality during migrations was probably typical.

By 1970, *A. californiense* had declined to near extinction at Lagunita. Interviews conducted in the early 1970s by SJB with dozens of Northern California herpetologists and collectors suggested that very few *A. californiense* remained at the lake. If migrations similar to those reported by Twitty were still occurring they would surely have been known to local collectors, who were quite interested in this animal because of its threatened status. Apparently, no Lagunita *A. californiense* were added to museums after 1955. SJB also palpated food samples from 35 common garter snakes (*Thamnophis sirtalis*) at Lagunita between 1972 and 1974 and found no adult or larval tiger salamanders. This snake is a primary *A. californiense* predator, and our experience in other areas indicates that they generally have larvae in their stomachs if salamanders are present. SJB also searched Junipero Serra Boulevard nearly every rainy night during January 1973 and 1974 and failed to locate any migrating adults. J. Gutstein (pers. comm.) searched Lagunita unsuccessfully in the late 1970s for *A. californiense*. The persons SJB interviewed generally and perhaps justifiably attributed the population decline to urban development, but L. Shapovalov, a 1931 Stanford graduate and later a California Department of Fish and Game fisheries biologist, believed that the salamanders had disappeared because some years there were fish in Lagunita.

On 3 June 1991, HBS seined eight tiger salamander larvae from the western border of Lagunita, and on 1 July 1992 he collected two individuals that were nearing metamorphosis. Allozyme comparisons (Stanley and Shaffer, unpubl.) confirmed that these are native *A. californiense* with the normal genotypes found in animals from the Bay Area. Thus, there is no reason to suspect that these are introduced salamanders, and they likely represent the same breeding population that was studied by Twitty 50 years ago. In January and February of 1992, M. Westphal of the U.S. Fish and Wildlife Service (pers. comm.) found two road-killed adult *A. californiense* on Junipero Serra Boulevard at

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Lagunita, and later in 1992 found several metamorphosed individuals in crevices in the sandbag embankment between the lake and the road. These discoveries confirm that the salamanders survive at Lagunita, but clearly there has been a drastic reduction in population size during the last 50 years.

A combination of factors have contributed to *A. californiense*'s decline at Lagunita. Post-World War II urban development is presumably responsible for some of it, because much of the land at Stanford and Palo Alto has been urbanized during that time. However, the aestivation hillside (approximately 13 ha) and Lagunita itself have been spared. Had either been modified the population would probably be extinct. Overcollecting may also have impacted the *Ambystoma* and *Taricha* populations adversely, especially because the available museum material probably represents only a fraction of what was actually collected up to 1955. However, this factor is difficult to assess, and there is no evidence that these salamanders were sought by the local pet trade.

We have found that Lagunita water management paradoxically sustains *A. californiense* reproductive activity, but probably destroys much of the annual recruitment. In normal rainfall years water accumulates in the lake bed during the winter, and the salamanders spawn in this shallow pool. However, annually for at least the last 50 years, Lagunita has been filled rapidly to at least 3 m in depth from San Francisquito Creek during a few days immediately prior to the April beginning of the Stanford Spring Quarter. Our observations elsewhere in the Bay Area indicate that by this time spawning is concluded, the breeding salamanders have left the lake, but larvae have not metamorphosed.

Until 1983, creek water entered the lake via the above-mentioned flume, but the flume was destroyed by heavy rains and later replaced by pumps and a pipeline. The original flume was protected by a screen with 2.5 cm (one-inch) mesh, and the current pipeline has a 6 mm (quarter-inch) mesh screen. Water in the Lagunita percolates into the underlying soil at a rate of almost two m^3/min. At that rate, the reservoir would recede rapidly to dryness by mid-June, but pumping from the creek continues in order to maintain the maximum water level, to allow use for recreation. The day after commencement exercises in June, a 26-cm drain (with a 5-cm mesh screen) in the bottom of the lake bed is opened and the lake is drained dry, at a rate of 15–30 m^3/min, over a 1–2-week period (L. Andrews, Stanford Water Department, pers. comm.). The water is returned via a storm drain to San Francisquito Creek and thence to the San Francisco Bay. Many, if not most, of the *A. californiense* larvae are probably swept down the drain to the creek, where predatory fish (e.g., rainbow trout, *Oncorhynchus gairdnerii*, and sculpin (*Cottus*) occur, and on to the bay, which is saline. During the warm summer the clay lake bed dries and cracks, grass grows for a time, and the grounds maintenance staff disc-plows the grass for aesthetic reasons and for fire prevention.

Fish are present in Lagunita, making it unique among over 300 potential breeding sites sampled by HBS since 1986 (Shaffer, unpubl. obs.). At all other sites fish are absent where *A. californiense* is present. SJB saw numerous suckers (*Catostomus*), a least 30 cm in length, wallowing in the muddy lake bed early in the summers of 1972 through 1974. HBS seined numerous goldfish (*Carrasius auratus*) from the remnant pool in 1991 along with salamander larvae. In 1992, he seined goldfish, adult threespine stickleback (*Gasterosteus aculeatus*), small suckers (*Catostomus*), guppies (*Lebistes*), and fathead minnows (*Pimephales promelas*) from Lagunita, along with salamander larvae. None of these are predatory fish, and all were less than 8 cm in length. They probably pass through the 6-mm mesh during the springtime creek pumping. Small trout, sculpins, and possibly warmwater predatory fish, such as largemouth bass (*Micropterus salmoides*), sunfish (*Lepomis*), and catfish (*Ictalurus*) (all of which are present in San Francisco Peninsula creeks) may also enter the lake via the pipeline. The large suckers seen in the 1970s are more difficult to explain, but they must somehow have breached or circumvented the original flume screen.

Ambystoma californiense larvae are generally well-developed by the time water is pumped into the reservoir in April, and during warm years may be approaching size to metamorphosis. Thus, the *timing* of water pumping into Lagunita is critical, for it is late enough to give the *Ambystoma* larvae a developmental head start over potential fish predators, and it ends late enough so that at least some larvae can metamorphose and become new recruits into the population. The entire Lagunita fish population is probably swept down the sump drain in June along with the salamander larvae, and the subsequent lake bed desiccation keeps reproductive fish populations from becoming established in the lake. This is probably the reason that the bullfrog, which prefers permanent or near-permanent water (Stebbins, 1951; Barry, unpubl. obs.) has not colonized Lagunita. This is important because these large, voracious frogs are known *A. californiense* predators (Anderson, 1968; Shaffer, unpubl. obs.).

A factor of unknown but probably substantial impact on the Lagunita *A. californiense* is mor-

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tality of migrating animals from passing automobiles. Fully 45% of the migrating animals reported by Twitty (1941) were road kills, and traffic has increased substantially on Junipero Serra Boulevard since 1940. Myers (unpubl.) also noted the high mortality from automobiles, and speculated that this might be a major cause of population decline at Lagunita.

Discussion and Recommendations

The management practices at Lagunita represent an interesting mix of activities which are both beneficial and detrimental to the long-term survival of *A. californiense*. Overall, the population has persisted for at least the last 52 years (from Twitty's 1941 observations to our own in 1991–1992), and probably for considerably longer, despite urban encroachment, possible overcollecting, automobile traffic, and breeding pool water manipulation. As such, it represents the longest example of a continuously managed, artificial habitat for the California tiger salamander, and it should serve as a model, both positive and negative, for other managed populations in northern California.

The two important, positive aspects of the management of Lagunita that we have identified are (1) the vary large size of both the aquatic and terrestrial habitat, and (2) the continuous filling *and draining* of the reservoir every year. These two conditions have apparently allowed the population in the past to grow to a large size, and have probably provided an important buffer against other, detrimental management practices and possibly against the impact of increased urbanization of the Stanford campus. Negative factors include the occasional introduction of fishes, death on roads from automobiles, discing the lake bottom annually, and draining the lake rapidly through a large, very high volume sump. In recent years, it appears that the negative aspects of this management scheme have reduced the population to a small size, and there may have been years in the 1970s and 1980s when little or no recruitment occurred. However, the population still exists, and we believe that it can be increased with a few key changes in management practices.

The Stanford University Administration is quite interested in preserving *A. californiense* at Lagunita. To date the Stanford Administration has agreed to mow rather than disc the grass in the dry lake bed during the summer, and has suspended plans for new building construction at Lagunita (D. Ullman, Stanford Planning Dept., pers. comm.). We agree that some metamorphosing larvae might burrow down into the lake bottom, and the mowing would be less hazardous to buried animals than would discing. Any further urban development at Lagunita is certain to impact the *A. californiense* population negatively.

It is most important to reduce the impact of automobile traffic on migrating animals and to minimize the loss of larvae during the lake drainage. A system of drift-fences combined with tunnels beneath Junipero Serra Boulevard would probably be the most efficient strategy to reduce automobile-related mortality during migrations. This system would provide a bidirectional migration corridor between the lake and the hillside aestivation area. Such routing systems have been used widely for anurans in Europe for at least 20 years (Ryser and Grossenbacher, 1989), and a fence-tunnel system has been used experimentally for *Ambystoma maculatum* in Massachusetts with encouraging results (Jackson and Tyning, 1989). A similar system of fences on the lake border could divert post-spawning and post-metamorphosing animals to the same tunnels so that they could reach the aestivation site.

A closer-mesh screen installed over the lake drain is an obvious preventive measure to protect the larvae from being flushed away, but it may not be feasible because such a screen would clog readily and be very difficult to keep clean during the drainage. Instead, perhaps the lake should be drained much more slowly, over a period of several weeks rather than only 7–14 d. In order to ensure that the maximum possible number of *A. californiense* larvae metamorphose, Lagunita should not be drained until midsummer. Our experience with the Hastings population indicates that larvae may not metamorphose until late July. Slow drainage of the lake at that time should allow most or all of the larvae to metamorphose, yet the lake would be emptied well before the commencement of the autumn rains.

Another approach would be to excavate a long, shallow ditch in the lake bed along the south edge of Lagunita. This would trap water and probably larvae as the lake is drained. Sumps could be excavated around the drain where larvae and water could collect during the drainage. These must be shallow enough to dry completely by midsummer, so that any fish also entrapped do not survive to the next rainy season. These sumps should be studied to determine if entrapped fish impact the *A. californiense* larvae. The ditch and sumps would probably require periodic re-excavation to counteract siltation.

All *A. californiense* aestivation areas around Lagunita should be identified and protected. There may even be opportunities to improve such aestivation areas by encouraging rodent populations, because their burrows are primary aestivation sites. Terrestrial habitat require-

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ments remain the least well understood component of the natural history of *A. californiense*, and additional data on burrow requirements and migration patterns are critical for a complete management and recovery plan.

Lagunita represents but a single *A. californiense* locality and some might question drastic efforts to preserve this population. However, this is apparently the last remnant of *A. californiense* on the San Francisco Peninsula. The nearest documented locality is in San Jose (uncatalogued specimens at California Academy of Sciences), some 30 km away, and that population is also in extreme danger of extirpation from development. Properly managed and protected, the Lagunita population could increase substantially. Unless the species and its specialized vernal pool habitat is protected from destruction under federal regulations, most of its remaining Bay Area populations (other than at Lagunita) probably will not survive very far into the 21st century. However, this need not be the case; as the survival of the Lagunita population demonstrates, salamanders and human activity can co-occur. Construction of a drift fence-tunnel system and implementation of minor changes in waterway management will likely result in much higher population levels at Lagunita. As such, we hope to see Lagunita become a model for the integration of vernal pool protection with human land use in northern California.

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