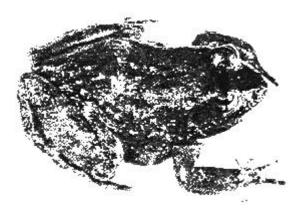
FOOTHILL YELLOW-LEGGED FROG (Rana boylii) Natural History

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The following is a literature review augmented with personal observations from several years of study of this species along a 39 mile stretch of the Trinity River, Trinity County, California. The study area extended from Lewiston Dam downstream to the confluence with the North Fork Trinity River near Helena. Personnel at the Redwood Sciences Laboratory conducted research with funding from the USDI Bureau of Reclamation.



OUTLINE

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- 3. Range and Distribution
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- 6. Movement and Dispersal
- 7. Habitat
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1. DESCRIPTION

The foothill yellow-legged frog (*Rana boylii*) is a moderate sized frog, with adults measuring 37.2 - 82.0 mm snout-urostyle length (SUL) (Jennings and Hayes 1994). The dorsal color is highly variable, but is usually a light and dark mottled gray, olive, or brown, often with variable amounts of brick red. The posterior portions of the abdomen and ventral surfaces of the rear legs are yellow, fading to white anteriorly. The yellow color is

absent on younger individuals (Leonard et al. 1993). The throat, chest, and posterior surfaces of the rear legs usually have dark mottling. During the breeding season, adult males have swollen nuptial tubercles on the medial surfaces of the thumbs to improve the grip during amplexus. The hind feet are fully webbed and toe tips are slightly expanded (Fig. 1).



In the Trinity River, *R. boylii* is easily distinguished from other local species by its rough skin, inconspicuous tympanum, horizontal pupils, fully webbed hind feet, poorly developed dorsal lateral folds, lack of dorsal stripe, lack of black eye mask, and its habit of jumping into flowing water for escape.

Newly hatched tadpoles are small and black and can be difficult to distinguish from young western toad tadpoles (*Bufo boreas*), which often occur in the same microhabitats as *R. boylii*. As the *R. boylii* tadpoles grow, they turn olive with coarse brown mottling dorsally. The ventral surface of the body is silvery and nearly opaque with the viscera barely visible. The body is somewhat flattened and the tail fin is dorso-ventrally reduced compared to other ranid tadpoles, possibly adaptations to living in lotic environments (Fig. 2) (Zweifel 1955, Nussbaum 1983). The tail fin is tallest at the mid-portion (Zweifel 1955). The posterior portion of the tail musculature usually lacks pigmentation (Corkran and Thoms 1996).



Drawings by Zweifel 1955.

The tadpole mouth also appears to be adapted for life in lotic river waters. It is large and orientated downward enabling the tadpoles to cling to rocks by suction (Corkran and Thoms 1996). The mouth is surrounded by labial tooth rows used for scraping algae and diatoms from rocks and plants. Labial tooth rows can be used for identification, however, recently hatched tadpoles have a tooth row configuration very similar to that of *B. boreas* tadpoles. About three weeks after hatching, the tooth rows have fully developed around the mouth and there are six or seven anterior labial tooth rows and five or six posterior labial tooth rows (Zweifel 1955, Leonard et. al. 1993) (Fig. 3). These tooth rows are the best way to positively identify mature *R. boylii* tadpoles, but they can be difficult to see even with the aid of a hand lens.

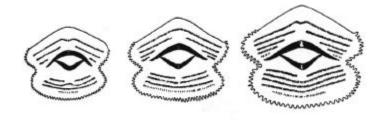


Figure 3. Time since hatching = 8 days; 12 days; 17 days. Drawings by Zweifel 1955.

Association with the parental egg mass remnant may be the best evidence of tadpole identity in the first week or so after hatching. By the second week after hatching, the egg mass remnant breaks down and the tadpoles disperse, making specific identification difficult if *R. boylii* and *B. boreas* are both present at the site. The tadpoles of these two species show slight differences in microhabitat preferences and escape behavior. Generally, *R. boylii* tadpoles flee more frantically and occur more often in moving water, whereas *B. boreas* tadpoles flee lazily and tend to occur in still water (pers. observ.). See figures in Stebbins (1985) for further morphological comparisons with *Bufo boreas* tadpoles.

2. TAXONOMY

R. boylii was first described by Baird (1854). A half century of taxonomic uncertainty followed with several name changes (Zweifel 1968). Since 1955, *Rana boylii* has been recognized as a distinct species in the family Ranidae (Zweifel 1955, Collins 1990). Zweifel (1955) described six species in the *R. boylii* group. *R. boylii*'s closest relative, both geographically and phylogenetically, is *Rana muscosa*. The four other ranids included in the *R. boylii* group by Zweifel (*R. pustulosa, R. tarahumarae, R. pueblae,* and *R. moori*) occur in Mexico, the latter extending into southern Arizona. Subsequent research suggests minor modifications to Zweifel's work on the *R. boylii* group (Dumas 1966, Green 1986a, Green 1986b). No subspecies of *R. boylii* are known to date, but detailed genetic analysis may reveal cryptic taxa (Jennings and Hayes 1994).

3. RANGE & DISTRIBUTION

Historically *R. boylii* occurred in most Pacific drainages west of the Sierra/Cascade Crest from the Santiam River, Marion Co., Oregon to the San Gabriel Drainage, Los Angeles Co., California (Jennings and Hayes 1988). Records exist for an isolated population in the Sierra San Pedro Martir, Baja California, Mexico (Loomis 1965). No *R. boylii* fossils are known (Zweifel 1968). Earlier this century *R. boylii* was described by Fitch (1936) as "probably the most abundant amphibian in the area" (Rogue River Basin, Oregon). In recent history the distribution and abundance of this species has been significantly reduced (*see* "status" below). In the main stem Trinity River, *R. boylii* is rare

in areas near the Lewiston Dam. In downstream areas, most of the frogs are clustered in the limited areas of suitable habitat (pers. observ.).

4. **REPRODUCTION and GROWTH**

In the spring, adult frogs congregate along gravel/cobble bar areas of the river, where breeding occurs. Previous literature reports breeding to occur from late March through May, with ovipositon for any single population being concentrated to a two week period (Storer 1925, Zweifel 1955). In the Trinity River, breeding activity occurs over a three month period from April through late June. While most oviposition occurs in May and early June (pers. observ., unpub. data), breeding is not limited to a two week period per breeding site. Oviposition may be delayed by the occurrence of rain during the breeding period (Kupferberg 1996a). This may be an adaptive response to life in a lotic system where *R. boylii* are exposed to the threat of late seasonal flooding. In the main stem Trinity River, this adaptive response for protecting egg masses from high flows may not be effective because high flow events are often disassociated with storm events (i.e. from dam releases; Lind et al. 1996).

While much of the mate calling occurs underwater (MacTague and Northern 1993), males also call from above water. Above water calls are faint and are not generally heard over distances greater than 50 meters (pers. observ.). Examples of both above water, and underwater calls are documented and described on <u>Frog and Toad Calls of the Pacific</u> Coast (Davidson 1995).

Oviposition usually occurs in the stream margin, at a depth of less than half a meter and with flow velocities of 0.0 to 0.21 m/second. Kupferberg (unpub. data) recorded flow

velocities as high as 0.55 m/second at the site of oviposition, although flows at the oviposition site were always less that of the adjacent thalweg (pers. observ.). There is some evidence that egg masses can withstand considerable flow, but this has not been quantified. Other evidence shows the loss of egg masses during high flow events (Lind et al. 1996) and *R. boylii* egg masses have also been found in nets on fish weirs during high flows (Michael Allen CDFG (916) 623-2800, pers. comm.). Cobble and pebble are the preferred substrate for egg mass attachment, but egg masses have been found attached to aquatic vegetation, woody debris, and gravel (Fuller and Lind 1992, pers. observ.).

Egg masses usually contain about 900 eggs, but the number of eggs can range from 100 to over 1000 per mass (Storer 1925). Upon deposition, the mass is compact within a clear to bluish gel. Within a few hours the egg mass absorbs water, loses the bluish tint, and expands to a fist-sized cluster resembling a bunch of tiny grapes. Each dark ovum is encased in three jelly envelopes (Fig. 4). The ova range in diameter from 1.0 to 2.3 mm and an ovum with its three jelly envelopes is about 5.4 mm in diameter (Zweifel 1955).



Figure 4. Ovum encased in three jelly envelopes.

Drawing by Zweifel 1955.

The developmental stage of the embryo can be observed using a 10X hand lens and assigned a number from Gosner's (1960) table of anuran embryo stages. Developmental rates are dependent on temperature. Within the species temperature tolerance range, development is probably accelerated with increased temperatures (Duellman and Trueb 1986). Eggs hatch in 5 to 30 days, or more (Zweifel 1955). In the main stem Trinity

River, eggs hatch in 27 to 36 days (pers. observ.). The slower development is probably due to colder temperatures from dam released water. At the time of hatching, the embyros are at a Gosner stage of 20 to 22 (pers. observ., Gosner 1960). In the absence of disturbance, the tadpoles will remain associated with the egg mass for several days after hatching. This can aid in species identification of young tadpoles, which look very similar to young western toad (*Bufo boreas*) tadpoles and occasionally share the same microhabitat in the Trinity River. In many species of amphibians, larval growth rate is also dependent on water temperature (Duellman and Trueb 1986) as well as food availability, but metamorphosis generally occurs in three to four months.

Maturity is attained by the time the frog is 40 mm SUL (Zweifel 1955). The reproductive organs commence activity in the first summer after metamorphosis and the first breeding activity usually occurs in the second postmetamorphic year (Zweifel 1955), although some individuals may reproduce as early as six months after metamorphosis (Jennings 1988).

There is little known on the longevity of amphibians in the wild (Duellam and Trueb 1986); the life span of *R. boylii* is essentially unknown. Van Wagner (1996) reported a recaptured female to be at least three years old. The life span may be a dozen years or more, based on studies of other ranids (Duellman and Trueb 1996).

5. FOOD HABITS

Rana boylii tadpoles feed on algae scraped from rocks or plants. They seem to grow fastest feeding on epiphytic diatoms and have been observed to preferentially graze on this algal type (S. Kupferberg pers. comm., Jennings and Hayes 1994). Tadpoles have been observed actively congregating on dead tadpoles and dead, open bivalves (pers.

observ.). The actual purpose of the behavior is unknown, but they appeared to be feeding, possibly on diatoms or algae on the corpses, or directly on the necrotic tissue.

In most frog species, the entire digestive system is reconfigured from a system for digesting small bits of plant material to a system for digesting large pieces of animal tissue during metamorphosis. No feeding occurs during this transformation (Duellman and Trueb 1986). The tail is re-absorbed by controlled cell death, which presumably is genetically programmed (Duellman and Trueb 1986).

Metamorphosed frogs feed primarily on terrestrial invertebrates, but also eat some aquatic invertebrates (Zeiner et al. 1988, Fitch 1936). Nussbaum (1983) reports the diet to include flies, moths, hornets, ants, beetles, grasshoppers, water striders, and snails. Van Wagner (1996) provides a thorough literature review and a detailed diet analysis of postmetamorphic *R. boylii*. In diet analysis of 63 post-metamorphic *R. boylii*, Van Wagner found terrestrial arthropods to be the primary (ca. 90%) prey items year round, comprised of 87.5% insects and 12.6% arachnids.

6. MOVEMENT and DISPERSAL

Little is known about movement and dispersal of this species (Jennings and Hayes 1994). Adults congregate around breeding pools in April, May, and June. Later in the summer adults are scarce along the main stem of the Trinity River (pers. observ.). This may indicate that they are dispersing into the vegetation, moving up tributaries, or reducing diurnal activity. Recently metamorphosed frogs show a strong tendency to migrate upstream (Twitty 1967). This may be an evolutionary mechanism to repatriate individuals washed downstream from suitable habitat during the larval stage.

Unless disturbed, upon hatching the tadpoles remain with the egg mass remnant for several days, then disperse to local interstices of the gravel bed, often moving downstream in areas of moderate flow (pers. observ.). The aquatic dispersal range for tadpoles has not been determined.

7. HABITAT

Several qualitative and quantitative descriptions of *R. boylii* habitat exist (Storer 1925, Fitch 1938, Zweifel 1955, Hayes and Jennings 1988, Kupferberg 1996a, Lind et al. 1996, Van Wagner 1996). *Rana boylii* breeding sites occur in shallow, slow flowing water with at least some pebble and cobble substrate (pers. observ., Fuller and Lind 1992). Pebble/cobble river bars along both riffles and pools, with at least some shading (>20%) seem to be preferred by sub-adults and adults. This species is also occasionally found in other in riparian habitats including moderately vegetated backwaters, isolated pools (Hayes and Jennings 1988, pers. observ.), and slow moving rivers with mud substrates (Fitch 1938).

8. PREDATION and MORTALITY

a. Predators

Rana boylii is susceptible to a wide range of predators from insects to mammals. Numerous aquatic insects are known to feed on anuran tadpoles, including larval odonates, predacious diving beetles, water bugs, and water scorpions (Milne and Milne 1980, Duellman and Trueb 1986). Garter snakes (*Thamnophis* sp.) are a primary predator of *R. boylii*. *Thamnophis couchi* preys heavily on tadpoles and postmetamorphic stages (Lind and Welsh 1994, Jennings and Hayes 1994, Nussbaum 1983). *Thamnophis sirtalis*

(Fitch 1941, Nussbaum 1983) and *T. elegans* also prey on postmetamorphic stages (Zweifel 1955). Everdon (1948) reported *Taricha granulosa* predation on egg masses of *R. boylii*. Bullfrogs have been implicated in declines of several anurans in the west, by both direct predation and competition for resources (Hayes 1985, Jennings 1988, Kupferberg 1996b, Hayes and Jennings 1986).

All life stages of *R. boylii* are susceptible to predation by various fish species and a variety of predatory fishes are suspected to feed on ranids (Jennings 1988). Centrarchid fishes are known to eat ranid eggs (Werschkul and Christensen 1977). Sacramento squawfish (*Ptychocheilus grandis*) prey on adult frogs and egg masses (Ashton and Nakamoto *submitted*) and in some areas tadpoles may constitute a significant portion of the *P. grandis* diet (Moyle and Brown 1997). The American Dipper (*Cinclus mexicanus*) is known to feed on *R. boylii* tadpoles (pers. observ.). Herons and even some passerine birds will feed on the tadpoles of a number of anuran species, as well as adults (Duellman and Trueb 1989). Mammalian predators such as raccoons may also forage opportunistically on tadpoles and frogs (Zweifel 1955).

b. Parasites

Fourteen species of helminth parasites were recovered from 150 specimens of *R*. *boylii* from Humboldt County, with 82.7% of the frogs hosting at least one species (Walker 1965). Walton (1964) lists at least nine other species of parasites occurring in *R*. *boylii* in Humboldt County.

c. UV-B exposure

Worldwide declines of amphibian populations have prompted researchers to investigate a range of possible environmental and atmospheric causes. Work with other ranids in the Pacific Northwest has shown a negative correlation between UV-B exposure and hatching success (Blaustein et al. 1994).

Recent evaluation of hatching success in relation to UV-B exposure in the eggs of *R. boylii* was inconclusive, primarily due to equipment damage and loss associated with storm events (Neumann 1997).

d. Drought & Dessication

During drought periods, frogs may be forced to congregate around remaining pools, leaving them more susceptible to predation (Moyle 1973, Hayes and Jennings 1988). Falling river levels also put eggs at risk of dessication by stranding them on land as the water recedes (Kupferberg 1996a). Desiccation of *R. boylii* egg masses along the main stem Trinity River study area has been documented in 1995, 1996, and 1997 (pers. observ.). These desiccations occurred as a direct result of the unnatural fluctuations in flow releases from the Trinity and Lewiston dams (see also Lind et al. 1996). Under natural flow regimes, *R. boylii* has be observed to oviposit earlier in the breeding season during drought years (Kupferberg 1996a).

e. Floods

High flows after oviposition can scour egg masses from the substrate. Losses by scouring have been documented in association with storm events and dam releases (pers. observ., Lind et al. 1996, Kupferberg 1996a). In Southern California, floods (estimated

to be of 500-year frequency) in 1969 may have been responsible for the extirpation of this species in the region (Sweet 1983).

f. Human Disturbance

Human disturbance and anthropogenic habitat loss can have significant effects on *R. boylii* populations. Some of these factors within the main stem Trinity River study site are discussed below in "Conservation, Threats in the Trinity River Basin."

9. CONSERVATION

a. Status

Rana boylii is a California Species of Special Concern (Jennings & Hayes 1994). Jennings and Hayes (1994) recommend endangered status in southern and central California south of the Salinas River, Monterey County, and threatened status in the "west slope drainages of the Sierra Nevada and southern Cascade Mountains east of the Sacramento-San Joaquin River axis." In the Coast Ranges north of the Salinas River *R*. *boylii* stills occurs in significant numbers in some coastal drainages (pers. observ.) but is at risk due to various anthropogenic and environmental threats. Thus it remains a Species of Special Concern in this region which includes the Trinity River (Jennings and Hayes 1994).

b. Threats in the Trinity River Basin

Unnatural flow regimes and loss of habitat since dam construction are the greatest threats to *R. boylii* on the main stem of the Trinity River. Since dam construction there has been a 94% loss of the potential *R. boylii* breeding habitat (Lind et al. 1996). Controlled flows have allowed the encroachment of riparian vegetation and retarded

cobble/gravel bar formation. Since dam construction water releases have been reduced to 10 to 30% of pre-dam flows, based on both total yearly volume and magnitude of periodic high flows (Lind et al. 1996). Decreased flows may force frogs into permanent pools where they are more susceptible to predation (Hayes and Jennings 1988). In several years, high flow releases from the dams late in the spring have resulted in scouring of egg masses. Alternatively, receding high flows, if poorly timed, can leave egg masses "high and dry" to desiccate in the sun (Lind et al. 1996, pers. observ.).

Logging and road related mass wasting events within the watershed have resulted in periodically high levels of siltation. High levels of silt may inhibit the attachment of the egg mass to the substrate. Excessive accumulation of silt on the egg masses may have adverse effects on embryo development, but this needs further study (Jennings and Hayes 1994). Silt reduces the interstitial spaces available for use by tadpoles, reduces algal growth on which the tadpoles feed (Power 1990), and can have a significant negative impact on aquatic macro-invertebrates (Petts 1984), in turn affecting the adult *R. boylii* prey base.

Introduced predators may also present a threat to *R. boylii* on the main stem Trinity River. Controlled flows and lack of winter flooding may actually increase suitable habitat for exotic bullfrogs (*Rana catesbeiana*) by providing stable pool areas with established aquatic vegetation (Lind et al. 1996, Kupferberg 1996b). The status of *R. catesbeiana* populations along the Trinity River is unknown.

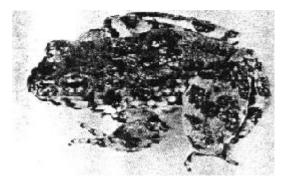
In the main stem Trinity River, there is evidence of fungal infections of amphibian egg masses, possibly *Saprolegnia* sp. (Blaustein et al. 1994, Kiesecker and Blaustein

1997). Fungal infection has been observed on *R. boylii* and *B. boreas* egg masses (pers. observ.).

The close proximity of State Highway 299 to the Trinity River poses the threat of toxic spills into the river. There are no restrictions on the type of materials which can be transported on Hwy 299 as long as approved packaging methods are employed (California Highway Patrol, Commerical Unit, (916) 225-2515, pers. comm.). Spillage of materials in transit into other nearby rivers has occurred in recent years (*e.g.* Upper Sacramento River at Cantara; Smith River off Hwy 199). Bury (1972) examined the effects of diesel fuel on a stream fauna in Northern California. He found negative impacts on *R. boylii* tadpoles and partially transformed individuals, but detected little impact on adult frogs.

Mining can have deleterious effects on egg masses and tadpoles, as well as disturbing postmetamorphic behavior patterns. Common mining methods along the main stem include panning, sluicing, dredging, and suction mining. The mining season on the Trinity River is open from 1 July to 15 October.

The problems discussed here are not unique to the Trinity River. Potential effects on *R. boylii* populations should be considered prior to and during any management



activities in or adjacent to aquatic habitat throughout its range. Many aspects of the life

history of R. boylii are in need of further study. Future research should address the issues

of habitat degradation and/or loss, flow regimes, and introduced aquatic predators.

LITERATURE CITED

- ASHTON, D. T. and R. J. Nakamoto. Submitted 1997. *Rana boylii* predation. Herpetological Review.
- BAIRD, S. F. 1854. Descriptions of new genera and species of North American frogs. Proceedings of the Academy of Natural Sciences of Philadelphia 7(2):59-62.
- BLAUSTEIN, A. R., P. D. Hoffman, D. G. Hokit, J. M. Kiesecker, S. C. Walls, and J. B. Hays. 1994a. UV repair and resistance to solar UV-B in amphibian eggs: A link to population declines? Proceedings of the National Academy of Sciences 91(5):1791-1795.
- BLAUSTEIN, A. R., D. G. Hokit, R. K. O'Hara, and R. A. Holt. 1994b. Pathogenic fungus contributes to amphibian losses in the Pacific Northwest. Biological Conservation 67(3):251-254.
- BROWN, L. R. and P. B. Moyle. 1997. Invading species in the Eel River, California: Successes, failures, and relationships with resident species. Environmental Biology of Fishes 49:271-291.
- BURY, R. Bruce. 1972. The effects of diesel fuel on a stream fauna. California Department of Fish and Game Bull. 58:291-295.
- COCKRAN, C. C., and C. Thoms. 1996. Amphibians of Oregon, Washington, and British Columbia: A field identification guide. Lone Pine Publishing. Vancouver, British Columbia, Canada. 175 pp.
- COLLINS, J. T. 1990. Standard common and current scientific names for North American amphibians and reptiles. Third Edition. Society for the Study of Amphibians and Reptiles, Herpetological Circular No. 19. 41 pp.
- DAVIDSON, C. 1995. Frog and toad calls of the Pacific Coast. Library of Natural Sounds, Cornell Laboratory of Ornithology. 159 Sapsucker Woods Road, Ithaca, NY 14850, USA. (607) 254-2404.
- DUELLMAN, W. E. and L. Trueb. 1986. Biology of the amphibians. McGraw-Hill Publishing Company. New York, NY. 670 pp.
- DUMAS, P. C. 1966. Studies of the *Rana* species complex in the Pacific Northwest. Copeia 1966(1):60-74.

- EVENDEN, F. G., Jr. 1948. Food habitats of *Triturus granulosus* in western Oregon. Copeia 1948(3):219-220.
- FITCH, H.S. 1936. Amphibians and reptiles of the Rogue River Basin, Oregon. Am. Midl. Nat. 17:634-652.
- FITCH, H. S. 1938. Rana boylii in Oregon. Copeia 3:148.
- FITCH, H. S. 1941. The feeding habits of California garter snakes. California Fish and Game 27:1-32.
- FULLER, D. D. and A. J. Lind. 1992. Implications of fish habitat improvement structures for other stream vertebrates. *In* R. Harris and D. Erman (eds.), Proceedings of the Symposium on Biodiversity of Northwestern California, pp 96-104. Santa Rosa, California.
- GOSNER, K. L., 1960. A simplified table for staging anuran embryos and larvae with notes on identification. Herpetologica 16(*):183-190.
- GREEN, D. M. 1986a. Sysematics and evolution of western North American frogs allied to *Rana aurora* and *Rana boylii*: Karyological evidence. Systematic Zoology 35(3):273-282.
- GREEN, D. M. 1986b. Systematics and evolution of western North American frogs allied to *Rana aurora* and *Rana boylii*: Electrophoretic evidence. Systematic Zoology 35(3):283-296.
- HAYES, M. P. 1985. *Rana catesbeiana* (Bullfrog). Food. Herpetological Review 16(4):109.
- HAYES, M. P. and M. R. Jennings. 1986. Decline of ranid frog species in western North America: are bullfrogs (*Rana catesbeiana*) responsible? Journal of Herpetology 20(4):490-509.
- HAYES, M. P. and M. R. Jennings. 1988. Habitat correlates of distribution of the California red-legged frog (*Rana aurora draytonii*) and the foothill yellow-legged frog (*Rana boylii*): implications for management. *In* R. C. Szaro, K. E. Severson, D. R. Patton (tech. Coords.), Management of Amphibians, Reptiles, and Small Mammals in North America, pp 144-158. USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, Gen. Tech. Rep. RM-166, Fort Collins, Colorado.
- JENNINGS, M. R. 1988. Natural history and decline of native ranids in California. Pp.61-72 *in* Proceedings of the Conference on California Herpetology. Eds. H. P. DeLisle, P. R. Brown, B. Kaufman, and B. M. McGurty.

- JENNINGS, M. R. and M. P. Hayes. 1994. Amphibian and reptiles species of special concern in California. California Department of Fish and Game, Final Report.
- KIESECKER, J. M. and A. R. Blaustein. 1997. Influences of egg laying behavior on pathogenic infection of amphibian eggs. Conservation Biology 11(1):214-220.
- KUPFERBERG, S. 1996a. Hydrologic and geomorphic factors affecting conservation of a river-breeding frog (*Rana boylii*). Ecological Applications 6(4):1322-1344.
- KUPFERBERG, S. 1996b. The ecology of native tadpoles (*Rana boylii* and *Hyla regilla*) and the impacts of invading bullfrogs (*Rana catesbeiana*) in a northern California river. Dissertation. University of California, Berkeley, California, USA.
- LEONARD, W. P., H. A. Brown, L. L. C. Jones, K. R. McAllister, and R. M. Storm. 1993. Amphibians of Washington and Oregon. Seattle Audubon Society, 168 pp.
- LIND, A. J., H. H. Welsh, Jr. 1994. Ontogenetic changes in foraging behaviour and habitat use by the Oregon garter snake, *Thamnophis atratus hydrophilus*. Animal Behaviour 48:1261-1273.
- LIND, A. J., H. H. Welsh, Jr., and R. A. Wilson. 1996. The effects of a dam on breeding habitat and egg survival of the foothill yellow-legged frog (*Rana boylii*) in northwestern California. Herpetological Review 27(2):62-67.
- LOOMIS, R. B. 1965. The yellow-legged frog, *Rana boylii*, from the Sierra San Pedro Martir, Baja California Norte, Mexico. Herpetologica 21(1):78-80.
- MacTAGUE, L. and P. T. Northern. 1993. Underwater vocalization by the foothill yellow-legged frog (*Rana boylii*). Transactions of the Western Section of the Wildlife Society 29:1-7.
- MEEHAN, W. R. (Editor). 1991. Influences of forest and range management on salmonid fishes and their habitat. American Fisheries Society Special Publication 19.
- MILNE, L. and M. Milne. 1980. The Audubon Society field guide to North American insects and spiders. Alfred A. Knopf, Inc. New York. 990 pp.
- MOYLE, P. B. 1973. Effects of introduced bullfrogs, *Rana catesbeiana*, on the native frogs of the San Joaquin Valley, California. Copeia 1973:18-22.
- MOYLE, P. B. and R. D. Nichols. 1973. Ecology of some native and introduced fishes of the Sierra Nevada foothill in central California. Copeia 1973:478-491.

- NEUMANN, J. R. 1997. Hatching success in relation to UV-B exposure in the eggs of the foothill yellow-legged frog. Unpublished Bachelor's Thesis, Department of Zoology, Humboldt State University, Arcata, California. 14 pp.
- NUSSBAUM, R. A., E. D. Brodie, Jr., and R. M. Storm. 1983. Amphibians & reptiles of the Pacific Northwest. University Press of Idaho. 332 pp.
- PETTS, G. E. 1984. Impounded rivers: perspectives for ecological management. John-Wiley and Sons. Chichester, Enland. 285 pp.
- POWER, M. E. 1990. Resource enhancement by indirect effects of grazers: Armored catfish, algae, and sediment. Ecology 71(3):897-904.
- STEBBINS, R. C. 1985. A field guide to western reptiles and amphibians. Peterson field guide series, Houghton Mifflin Company, Boston.
- STORER, T. I. 1925. A synopsis of the amphibia of California. University of California Publication Zoology 27:1-342.
- SWEET, S. S. 1983. Mechanics of a natural extinction event: *Rana boylii* in southern California [abstract]. Program of the 26th Annual Meeting of the Society for the Study of Amphibians and Reptiles and 31st Annual Meeting of the Herpetologists League at the University of Utah [August 7-12]:93.
- TWITTY, V. C., D. Grant, and O. Anderson. 1967. Amphibian orientation: An unexpected observation. Science 155(3760):352-353.
- VAN WAGNER, T. J. 1996. Selected life-history and ecological aspects of a population of foothill yellow-legged frogs (*Rana boylii*) from Clear Creek, Nevada County, California. Master's Thesis, Department of Biological Sciences, California State University, Chico. 143 pp.
- WALKER, Michael E. 1965. A survey of helminth parasites of *Rana boylei* from Humboldt County, California. Master's Thesis, Humboldt State University.
- WALTON, A. C. 1964. The parasites of amphibia. Wildlife Disease Association, number 40.
- WERSCHKUL, D. F. and M. T. Christensen. 1977. Differential predation by *Lepomis macrochirus* on the eggs and tadpoles of *Rana*. Herpetologica 33:237-241.
- ZEINER, D. C., W. F. Laudenslayer, Jr., and K. E. Mayer, eds. 1988. California's wildlife, volume 1, amphibians and reptiles. California Department of Fish and Game. 272 pp.

- ZWEIFEL, R. G. 1955. Ecology, distribution, and systematics of frogs of the *Rana boylii* group. Univ. of California Publ. Zool. 54:207-292.
- ZWEIFEL, R. G. 1968. *Rana boylii* Baird, Foothill yellow-legged frog. Catalogue of American Amphibians and Reptiles. Pp. 71.1-71.2.