ARTICLES

The Effects of a Dam on Breeding Habitat and Egg Survival of the Foothill Yellow-legged Frog (*Rana boylii*) in Northwestern California

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Although the debate continues on the relative roles of natural fluctuations and anthropogenic influences in recently observed amphibian population declines (Blaustein 1994; McCoy 1994; Pechman et al. 1991; Pechman and Wilbur 1994; Travis 1994), many species are clearly demonstrating local extinctions and large-scale declines (Blaustein and Wake 1990; Blaustein et al. 1994b; Fellers and Drost 1993; Hayes and Jennings 1986; Jennings 1988). Causes of these declines can be placed in two broad categories: direct habitat degradation (Blaustein et al. 1994b), and more nebulous large-scale environmental changes and contamination (e.g., airborne pollutants, acid precipitation, ultraviolet radiation) (Blaustein et al. 1994a; Dunson and Wyman 1992; Fellers and Drost 1993; Hagstrom 1977; Harte and Hoffman 1989).

Dams and water diversion projects have been proposed as causes of declines of many native frogs (Hayes and Jennings 1986; Jennings 1988;Moyle 1973), but the effects of these projects have not been quantitatively evaluated. Water diversions also have been implicated in region-wide declines of anadromous fish in the Pacific Northwest (Moyle and Williams 1990; Nehlsen et al. 1991) and are documented to adversely affect riverine macroinvertebrates (Petts 1984). Impacts to fish include loss and degradation of habitat because of reservoir filling and downstream changes in river morphology along with detrimental off-season andfluctuatingwaterreleases(BurtandMundie 1986; Petts 1984). A recent petition to list the arroyo southwestern toad (*Bufo microscaphus califomicus*) as endangered indicated that impoundments associated with dam construction have caused a 40% loss in the original habitat of this toad. In addition, it was suggested that habitat quality downstream of dams has been severely compromised by changes hi water temperatures, riparian vegetation, and habitat stability (Federal Register 1993). Our study provides information on both direct and indirect effects of a dam on the foothill yellow-legged frog (*Rana boylii*) in a northwestern California river system.

Rana boylii is generally found in association with stream riffles that have rocky substrates and partly shaded banks (Hayes and Jennings 1988; Moyle 1973; Zweifel 1955). This frog ranges from northern Baja California, Mexico (Loomis 1965) to central Oregon, west of the Sierra Nevada and Cascade crests. *Rana boylii* is currently listed as a Species of Special Concern in California (Laudenslayer et al. 1991) and is also a candidate for Federal listing (Federal Register 1994). The most notable declines are in southern California and the west slope drainages of the Sierra Nevada and southern Cascade Mountains (Jennings and Hayes 1994; Leonard et al. 1993).

Our objectives were: (1) to describe the changes in *Rana boylii* breeding habitat in a dammed river prior to and some years following dam construction, and (2) to document the effects of the timing of water releases from the dam on the reproductive ecology of this population.

Our study took place on the main stem of the Trinity River, in Trinity County, California, USA, and covered the 63 km of river from Lewiston Dam (near Lewiston, California) downstream to the confluence with the North Fork Trinity, near Helena, California (elevation 420-550 m). Construction of two dams, an upper (Trinity) and a lower (Lewiston), was completed in 1963. At Helena, this river drains an area of 2968 km^2. Before dam construction the river had an average yearly (water year, Oct-Sept) discharge of 1.2 million acre-feet at Lewiston. During the four years of our study, the yearly discharge ranged from 270,800 to 367,600 acre-feet at Lewiston. The basin surrounding our study reach is 52% public land (USDA Forest Service and USDI Bureau of Land Management) and 48% privately owned. Land use activities within this watershed include logging and associated road building, recreation, and widely scattered home construction. Portions of river channel and adjacent areas were mined in the early to mid-1900's.

Since 1984, the USDI Fish and Wildlife Service, in cooperation with the USDI Bureau of Reclamation (the dam administrator), has been conducting a flow evaluation study on the main stem of the Trinity River. Water has been released at varying levels above base flow (8.5 m^3/sec [cms]), each spring in order to facilitate migration of wild and hatchery-raised anadromous fish and to permit evaluation of fish habitat availability and changes as a function of discharge. The timing of these high flow releases has been influenced by many factors, though efforts have been made to mimic historical flow release patterns (Trinity River Restoration Program 1994).

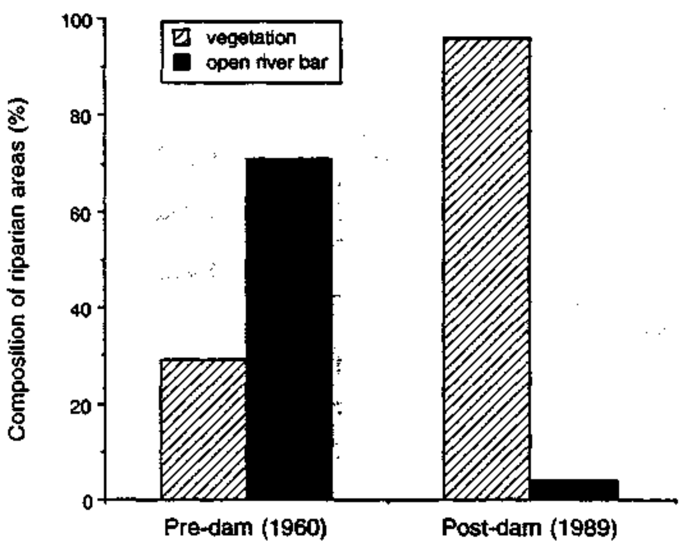

FIG. 1. Riparian habitat composition before (1960) and 26 years after (1989) construction of Trinity and Lewiston Dams on the main stem Trinity River. Estimates were derived from GIS analysis of aerial photo graphs.

A geographical information system (GIS) was used to analyze amount and distribution of riparian habitats prior to and following construction of the dams. Aerial photographs taken before (1960) and 26 years after (1989) the construction of the dams were used to derive estimates of the areal extent of four riparian habitats: (1) unvegetated rocky areas, (2) willow stands, (3) willow/alder mixed stands, and (4) alder/cottonwood stands. We used U.S. Geological Survey (USGS) records of flow releases at Lewiston and in an undammed tributary stream within our study area, Grass Valley Creek, California, to determine the riming and magnitude of discharges during our study. Values for discharge at Helena (the lower end of our study area) were derived by extrapolating tributary flows from Grass Valley Creek to the drainage area between Lewiston and Helena.

Held surveys of all potential breeding habitat were conducted from 1991-1994 along the study reach described above. Designation of potential breeding habitat was based on literature accounts of suitable habitat (Fuller and Lind 1992; Hayes and Jennings 1988; Kupferberg, in press; Zweifel 1955) and our experience with this species in other drainages in northwestern California. Potential breeding habitat, for riverine environments, was defined as low-velocity (0.0-0.21 m/sec), shallow water (8-40 cm), with rocky substrates, adjacent to sparsely vegetated, gravel/cobble bars (hereafter referred to as bars). Bars are formed through the natural meandering process of rivers and are areas of repeated sediment deposition and erosion; usually they occur on the inside of meander bends (Leopold et al. 1964). We sampled only those bars (= sites) that were at least 10 m long and composed of coarse gravel (>32 mm diam: Plaits et al. 1983) or larger substrates. Many of the bars are no longer geomorphologically active because of decreased flows. In these cases, only the sparsely vegetated portions of bars were surveyed and the heavily vegetated and steeply sloped portions were omitted because of poor habitat quality. In 1993 and 1994, we also surveyed several "bank feathering" restoration projects that were within our study reach. These feathering projects are designed to restore river bars to their historic form. Through removal of riparian berms and encroaching vegetation, river banks are mechanically recontoured to form a gentle slope and provide shallow, low water-velocity habitats (Trinity River Restoration Program 1994).

Several surveys were conducted throughout the breeding and rearing season of *Rana baylii* on the main stem Trinity River in 1991-1994 (Table 1). Two surveys were conducted each spring in 1991-1993 and one in 1994. Twenty-five to 33 natural bars were surveyed each year. In addition, one bank-feathering project was surveyed in 1993 and five more were surveyed in 1994. Surveys were timed to coincide with the peak of breeding activity each year, if possible, and were carried out from late April through

TABLE 1. *Rana boylii* reproductive ecology on the main stem Trinity River, between Lewiston and Helena, in northwestern California, 1991-1994.

Year	Survey Type	Survey Dates	Km	# Sites	#With Egg Masses	Total # Masses	# Masses /Km
1991	Initial	May 2-14	62.8	47	4	7	0.1
	Potnl Breed Sites	May 15-24	22.5	31	7	31	1.4
	Post-high flow	Jun 4-6	—	7	0	0	—
	Post-high flow	Jun 7-14	—	7	1	3	—
	Post-high flow	Jun 17-21	—	7	1	1	—
	Larvae (egg sites)	Jul 31-Aug 30	—	7	(2)[1]	—	—
	Larvae (other sites)	Jul 31-Aug 30	62.8	47	(11)	—	—
1992	Potnl Breed Sites	Apr 28-May 7	16.1	25	3	7	0.4
	Potnl Breed Sites	May 26-Jun 4	16.1	25	10	28	1.7
	Post-high flow	Jun 25-26	—	10	0	0	—
	Larvae (egg sites)	Jul 28-29	—	10	(3)	—	—
1993	Subset Potnl Breed	Jun 9-Jun 28	—	13	0	0	—
	Potnl Breed Sites	Jul 7-Jul l5	22.5	34[2]	0	0	0.0
	Larvae	Aug 30-Sept l	22.5	34	(8)	—	—
1994	Potnl Breed Sites	Jun l-Jun 9	22.5	39[3]	11	24	0.9
	Monitoring Site	Apr 15-Nov 14	—	1	12		—

1. ( ) = larvae only found at this site.
2. Includes one recently completed bank feathering restoration project she-and two natural sites not surveyed in previous years.
3. Includes five recently completed bank feathering restoration project sites not surveyed in previous yean; 10 of 24 egg masses were laid at these sites.

June. At least one mid-summer survey (late July/early August) was conducted to search for larvae. We also conducted at least one survey at known breeding sites, immediately following high-flow releases from the dam to track egg mass survival. In 1993, high-flow releases from Lewiston Dam in April were followed by a long period of rain and natural high flows from tributary input in May and early June; as a result we surveyed substantially later than in other years. At each bar site, egg masses, juveniles, and adult frogs were counted. The length of each bar was measured by pacing so that estimates of frogs and egg masses per linear meter of habitat could be derived. We also examined historical locality records for *Rana boylii* to qualitatively assess the distribution of this species in the Trinity Basin prior to dam construction on the main stem.

Water releases since construction of the dams have been 10-30% of pre-dam flows, based on both total yearly volume and magnitude of periodic high flows (Trinity River Restoration Program 1994; USGS records 1991-1994). Within our study area, vegetation covered less than 30% of the pre-dam riparian area and more than 95% of the post-dam area. Open bars made up 70% of the pre-dam riparian area and only 4% of the post-dam area (Fig. 1). This constitutes a loss of 94% of bar habitat, and potential breeding habitat for *Rana boylii.* Encroachment by riparian vegetation has resulted hi the development of stable sandy berms, forcing the river into a narrower and deeper channel that lacks habitat complexity. Other changes seen along the main stem Trinity include loss of seasonally flooded marshes and high-flow side channels, filling of pools with fine sediments, lowered water temperatures, and riffle sedimentation (Petts 1984).

Historical records (Bury 1967; Museum of Vertebrate Zoology, University of California at Berkeley) demonstrate that *Rana boylii* occurred on the main stem Trinity and in many tributary streams, though relative abundance could not be gauged from these records. Initial surveys indicated that there were few *Rana boylii* in the upper portion of our study area and that the lower section had more potential breeding habitat due to the more natural flow conditions created by tributary streams; subsequently we surveyed only the lower 22.5 km. Of the 25-39 bar and bank feathering sites searched, 7-10 had egg masses annually. Total egg mass counts over four years ranged from 21-31 annually in 22.5 km (Table 1).

During the four years we tracked breeding relative to the tim-

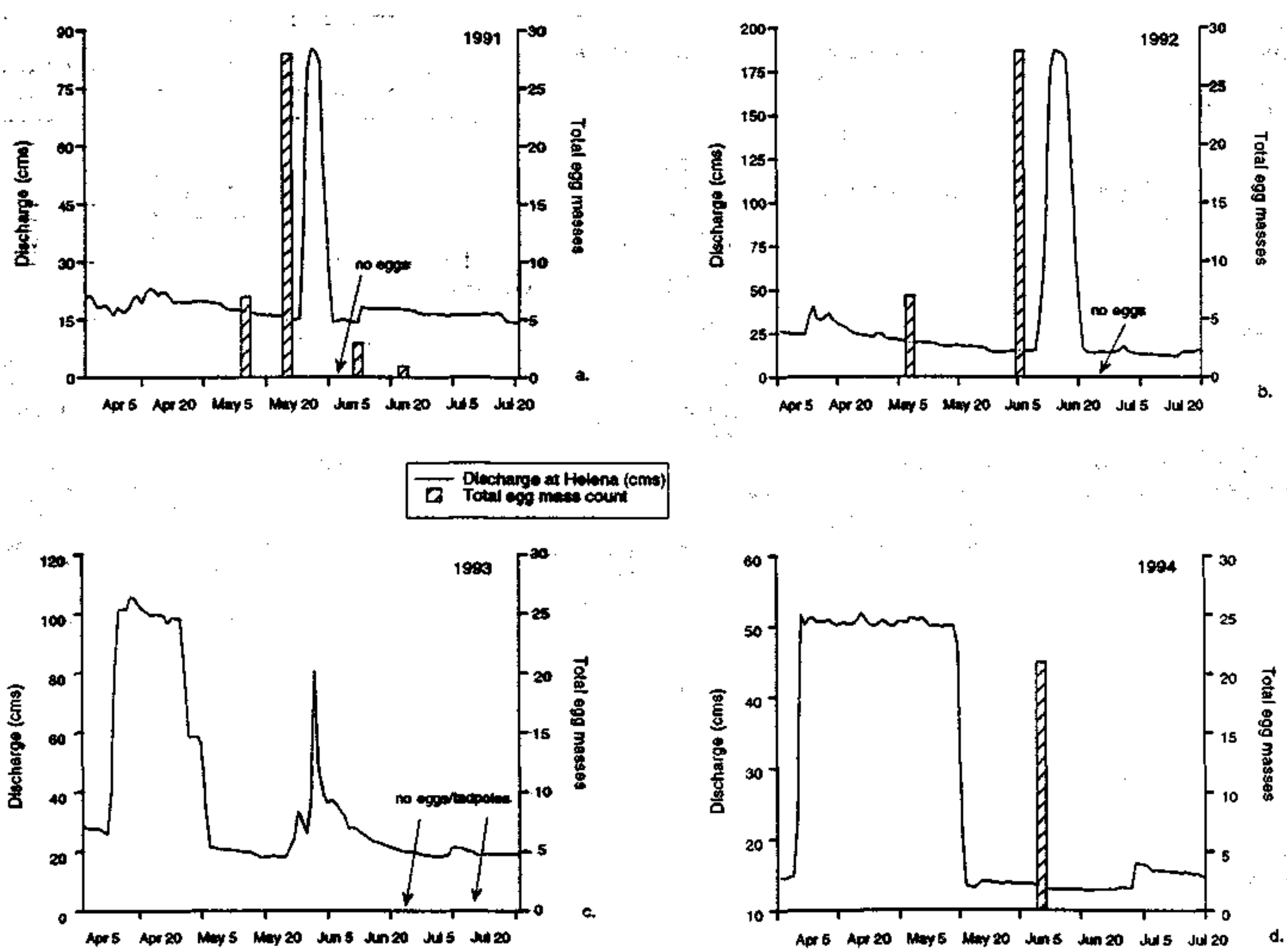

FIG. 2. Chronology of foothill yellow-legged frog (*Rana boylii*) breeding and egg mass abundance as documented by river shoreline surveys, and discharge (in cubic-meters per second [cms]) of the main stem Trinity River at Helena for (a) 1991, (b) 1992, (c) 1993, and (d) 1994.

ing and magnitude of flow releases on the main stem, we found significant negative impacts in 1991 and 1992 and undetermined impacts in 1993 and 1994. In 1991 and 1992, all egg masses laid before high flow releases were lost (Table 1, Fig. 2a & b). In 1991, three egg masses were laid at one site after the largest flow release, and a second flow increase from 14 to 18 cms eliminated two of the three (Fig. 2a). Mid-summer surveys of breeding sites indicated that larvae survived after the high flows only at sites where egg masses had hatched prior to high-flow releases. In 1991, three to four larvae were found at two of the seven known breeding sites. Of the 10 known 1992 breeding sites, three sites had one larvae each and three sites had two, eight, and fifteen larvae. In 1993 we found no egg masses or larvae during spring surveys, though surveys were conducted later than in previous years. However, we did find larvae at several sites during mid-summer surveys. We do not know whether these larvae were missed during spring surveys or whether they moved into the main stem from unsurveyed tributary streams. The only year in which a substantial proportion of egg masses and larvae appear to have survived to metamorphosis was 1994. High-flow releases were earlier in 1994, and most breeding activity occurred after these releases (Fig. 2d). At one site visited biweekly through late October 1994, all life stages were seen, though no more than two metamorphic individuals were seen on any given day.

Though downstream effects of dams can be quite variable, several changes appear consistent across most dammed systems. For example, peak flood flows are decreased and year-round flows are typically lower (Ligon et al. 1995; Williams and Wolman 1984). Sediment concentrations and suspended sediments decrease substantially for many miles downstream and bed material typically becomes more coarse (Ligon et al. 1995; Williams and Wolman 1984). In general, the areal extent of riparian vegetation increases below dams as a result of reduced flows and lack of scouring floods; this was the case on the Trinity (Fig. 1, Petts 1984). In addition, riverine species experience direct habitat loss as a result of reservoir filling. Erode and Bury (1984) documented a potential loss of more than 50 km of stream habitat for *Rana boylii* inhabiting the area of a proposed dam and reservoir.

On the Trinity River, two aspects of the dams are having significant impacts on the *Rana boylii* population. First, river morphology has changed significantly since flows became controlled in 1963, and as a result a significant amount of breeding habitat has been lost (Fig. 1). Data from a comparably-sized undammed river fork in the same system (the South Fork Trinity) demonstrated that both the number of potential sites and the total number of egg masses were substantially higher on this fork than in our main stem study area. We found 548-730 egg masses annually, at 81-87 sites in 15 km during three years of surveys from 1992-1994 on the undammed fork (unpublished data). The second factor is the timing of high-flow releases from the dam. In at least two of the last four years, entire cohorts of *Rana boylii* were lost along our main stem study reach because of unseasonal high flow releases (Fig. 2). Kupferberg (in press) demonstrated that survival of *Rana boylii* egg masses in a natural river was dependent on channel morphology and timing of egg deposition, during both increases and reductions in flows.

Other dam-related factors that may influence the breeding ecology of *Rana boylii* in this river are water temperature, exotic species, and changes in prey base. To accommodate fisheries requirements, water temperatures are kept artificially low (relative to pre-dam conditions and present conditions on other local rivers) using higher than normal releases in mid-summer; this may retard development of eggs and larvae (Duellman and Trueb 1986).

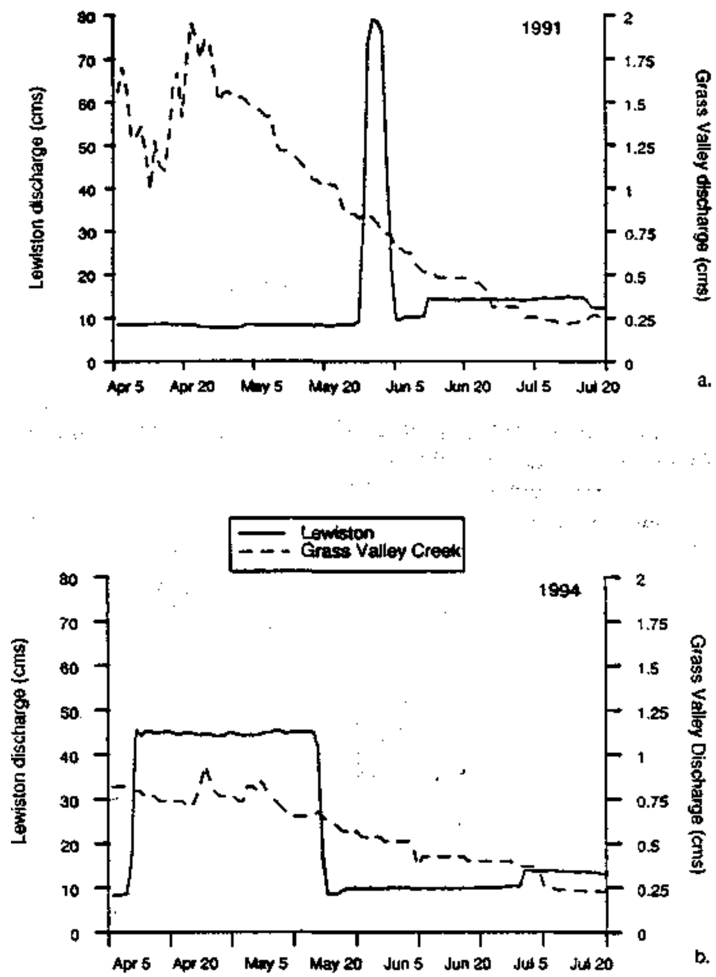

FIG. 3. Discharge (in cubic meters per second [cms]) hydrographs for the main stem Trinity River at Lewiston, and Grass Valley Creek, a tributary to the main stem below Trinity and Lewiston dams for (a) 1991 and (b) 1994.

Bullfrogs (*Rana catesbeiana*), a suspected predator on many native western ranids (Hayes and Jennings 1986; Moyle 1973), are present hi the main stem Trinity (pers. obs.). Controlled flows and lack of winter flooding may actually increase suitable habitat for this exotic frog by providing stable pool areas with established aquatic vegetation. Changes in macro-invertebrate prey composition and abundance have been documented in many dammed river systems (Petts 1984) and these changes may affect native amphibians.

We believe the negative impacts we have identified on the main stem Trinity River can be reduced with thoughtful management. Habitat loss is a critical problem and *Rana boylii* has responded to "bank feathering" restoration projects within one year of construction. Ten of the 24 egg masses found hi 1994 surveys were at restoration sites. However, we do not know whether frogs using these newly created habitats are additions to the breeding population or whether the frogs have moved into these areas simply because they are more suitable than what is currently available on the river.

Tuning of high flows is more difficult to address because we do not know what environmental or other cues frogs use to initiate breeding. The timing of amphibian breeding is thought to be influenced by factors such as temperature and day length, which directly affect hormonal cycles (see Duellman and Trueb 1986 for a review). Metter (1961) speculated dial for western toads (*Bufo boreas boreas*) breeding in riverine systems, timing and volume of run-off may also influence timing and location of breeding. An Asian stream-breeding frog, *Buergeria buergeri,* is known to decrease its breeding activity during heavy rainfall and high stream flows (Fukuyama and Kusano 1992). On the main stem Trinity, releases usually have been timed to mimic *average* predam patterns of spring run-off events. Using average conditions to determine flow schedules may or may not be consistent with environmental conditions in a given year. Fof example, if a threshold temperature or water level is required before frogs can initiate breeding and these conditions occur in April because of local climatic shifts, frogs may initiate breeding. If high-flow releases then occur in May of that year, egg masses or larvae are likely to be lost Compare the discharge from an undammed tributary within the watershed to controlled discharges from Lewiston dam for the same time period in 1991 and 1994 in Figure 3. The tributary stream reflects the natural environmental conditions. In 1991 (and 1992, not shown), high flow releases from the dam occurred much later than the natural flow regime demonstrated by the tributary and in 1994 timing was similar between the main stem and the tributary. Note that 1994 was the only year hi which we believe that a substantial portion of larvae survived to metamorphosis. A more appropriate strategy for *Rana boylii* and, we suspect, for most species that have evolved hi stochastically fluctuating riverine environments, would be to base real-time changes in flow releases on current environmental conditions (e.g., if it is raining, release more water). Understanding the interactions between environmental factors (both natural and artificial) and frog breeding ecology is critical for managing water releases to reduce impacts on frogs and other species existing in dammed river systems.

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Prey of the Introduced *Bufo marinus* on American Samoa

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The giant cane or marine toad, *Bufo marinus,* is native to Central and northern South America (Zug and Zug 1979) but has been widely introduced to islands in the West Indies, the Pacific, Australia, and New Guinea (reviewed by Zug et al. 1975). In many areas it was introduced primarily to control sugar cane insect pests and has apparently been fairly successful hi some areas in reducing damage to this crop (Wolcott 1937).

Bufo marinus was introduced from Hawaii to Tutuila Island (14°20'S, ITO^S'W), American Samoa, in 1953 and the population was estimated to be over 2 million by 1976 (Amerson et al. 1982). Toads occur island-wide on Tutuila, have colonized neighboring Aunu'u Island, but do not presently occur on the nearby islands of Tau, Ofu, and Olosega, nor on Savaii and Upolu of Western Samoa.

Marine toads have catholic tastes (Alexander 1965; Hinckley 1963; McCoid 1994; Zug et al. 1975). The purpose of this study was to examine the food habits of marine toads in two different habitats on Tutuila, American Samoa.

On Tutuila Island, 26 toads were collected in suburban and park areas in the village of Tafuna and 28 were collected in secondary forest and primary rainforest (forest) of Amalau and Olovalu Crater near Futiga. Toads were collected from 24 October 1992 to 13 July 1994 and always 2-4 h after sunset to allow some time for foraging by the toads. Collected toads were immediately placed in plastic bags and frozen until processing.

Table 1. Mean (standard deviation) snout-vent lengths (SVL), jaw width (JW), and body mass minus stomach contents (BM) for 54 *Bufo marinus* in two habitats on Tutuila, American Samoa. Probabilities based on unpaired t- test

	Combined N=54	Suburban/Park N=26	Forest N=28	P
SVL (mm)	97.2(13.9)	88.5(11.9)	105.4(10.2)	0.000
JW (mm)	36.9 (5.5)	33.8 (4.9)	39.8 (4.3)	0.000
BM(g)	90.6(41.8)	68.0(29.9)	111.6(37.0)	0.000

Table 2. Mean (standard deviation) weight of entire contents, animal contents, and plant/grit contents from stomachs of *Bufo marinus* from two habitats on Tutuila, American Samoa. Probabilities based on t- tests.

	Suburban/Park N=26	Forest N=28	P
Entire contents (g)	2.3(1.8)	4.7(3.2)	0.001
Animal contents (g)	1.3(1.7)	2.9(2.1)	0.004
Plant/grit contents (g)	1.0(1.2)	1.8(1.9)	0.058

Intact toads, entire stomach contents, animal content of stomachs, and plant/grit content of stomachs were weighed to the nearest 0.1 g on a triple-beam balance. Snout-vent length (SVL) and maximum width of the jaws was measured with dial calipers to the nearest 0.1 mm. Animal prey were identified to the lowest possible taxonomic level and quantified.

Forest toads were longer, had wider gapes, and weighed more than suburban/park toads (Table 1). In addition, the stomachs of forest toads contained twice as much food by mass as did those of suburban/park toads. Animal contents, but not plant/grit contents, of the stomachs were significantly greater in forest toads (Table 2).

Toads in both habitat types took a wide variety of prey (Table 3). Nearly one half of the prey taken by forest toads was millipedes, whereas suburban/park toads took more moths, caterpillars, and beetles. The largest centipede taken was 51 mm long. Termites, geckos, and dog food were also eaten by toads in suburban/park habitats (P. Craig, B. Grant, P. Trail, pers. comm.), but the latter two items were not found hi the stomachs of this study. Nearly equal numbers of animal prey were found in suburban/park toads (227) as in forest toads (217). Because the animal con-