Habitat Correlates of Distribution of the California Red-Legged Frog *(Rana aurora draytonii)* and the Foothill Yellow-Legged Frog *(Rana boylii)*: Implications for Management[1]

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Abstract.—We examined features of the habitat for the California red-legged frog and foothill yellow-legged frog from the Central Valley of California. Limited overlap exists in habitat use between each frog species and introduced aquatic macrofaunal predators. Temporal data implicate aquatic predators that restrict red-legged frogs to intermittent stream habitats as explaining limited overlap. Identification of responsible predators is currently prevented because the alternative of limited overlap simply due to differential habitat use between frogs and any one putative predator cannot be rejected. Until the predators causing the negative effects are identified, efforts should be made to isolate these frogs from likely predators and minimize alteration of key features in frog habitat.

The application of habitat analysis to management has a long, complex history. The Greek philosopher Aristotle inferred that seasonal variation in the distribution of certain commercially exploited fishes was related to changes in their food resources and habitat temperatures (Cresswell 1862). In the 13th century, the Mongol emperor Kublai Khan encouraged the gathering of data on foraging patterns of sport-hunted birds to facilitate manipulating their populations (Leopold 1931). Since these efforts, many individuals have used diverse habitat data to help understand factors that influence the distribution and success of various species. Most often, such data have been used to address commercially important or game species, usually to identify management alternatives intended to enhance existing populations or avert population declines (Bailey 1984, Leopold 1933). This emphasis has resulted in most studies addressing selected birds, fishes, and large mammals. In contrast, species historically having limited economic importance (i.e., "non-game" species) have been largely neglected (Bury 1975; Bury et al. 1980a, b; Pister 1976). Only over the last 15 years has an appreciation been broadly realized that non-game species are also in need of management. Non-game species are often linked to economically important ones, and as such, provide significant direct and indirect benefits to humans (Kellert 1985, Neill 1974). Although this appreciation has led to greater emphasis in their study (Bury et al. 1980a, Pister 1976), a broader understanding of the biology of non-game species is increasingly urgent because of widespread habitat modification influencing declines among ever-greater numbers of such species (Dodd 1978, Hayes and Jennings 1986, Hine et al. 1981, Honegger 1981).

Amphibians are prominent among groups of organisms given a non-game label (Bury et al. 1980a). For ranid frogs, among the most familiar of amphibian groups, non-game is really a misnomer (Brocke 1979) because they have a history of human exploitation which has its roots in European and aboriginal cultural traditions (Honegger 1981, Zahl 1967) and has included significant commercial enterprises (Abdulali 1985, Chamberlain 1898, Husain and Rahman 1978, Jennings and Hayes 1985, Wright 1920). Despite this history of exploitation, few attempts have been made to link species-specific habitat requirements of ranid frogs to their management (but see McAuliffe 1978; Treanor 1975a, b; Treanor and Nicola 1972). Most "management" literature has either simply reviewed the biology of selected ranid frog species or indicated vulnerable life history stages needing study (Baker 1942, Bury and Whelan 1984, Storer 1933, Willis et al. 1956, Wright 1920).

In this report, we examine the habitat features of two "non-game" species, the California red-legged frog *(Rana aurora draytonii)* and the foothill yellow-legged frog *(Rana boylii)*, two ranid frogs found in lowland California. Each species has disappeared from sizable areas of its historic range (Hayes and Jennings 1986, Sweet 1983). Although historical disappearance of red-legged frogs has been linked to its exploitation as food (Jennings and Hayes 1985), causal factors in the continuing decline of both species remain poorly understood. Insufficient documentation of the habitat requirements of each species has especially impeded identification of the causes of decline (Hayes and Jennings 1986). In this report, we reduce this gap by identifying the habitat requirements that characterize each frog. We then use these data to suggest the direction for management of these two species

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until experiments can identify the causes of decline.

METHODS

Our analysis draws upon two data sets, one addressing *R. a. draytonii* and the other, *R. boylii*. The former is based on all known occurrences of *R. a. draytonii* (n = 143) from the Central Valley of California, which we define as the collective drainage area of the Kaweah, Kern, Sacramento-San Joaquin (to Carquinez Strait), and Tule River systems. We assembled these data from museum records and field notes or direct observations of the many investigators listed in the acknowledgments or whose data are cited in Childs and Howard (1955), Cowan (1979), Fitch (1949), Grinnell and Storer (1924), Grinnell et al. (1930), Hallowell (1854, 1859), Ingles (1932a, b; 1933; 1936), Storer (1925), Walker (1946), Williamson (1855), and Wright and Wright (1949). We used records not authenticated by museum specimens if they were corroborated by at least two sources. We then determined the subset (n = 131) of records that could be both mapped (i.e., where we could identify the aquatic system likely to be the site of origin of the source population upon which the record was based), and identified as being from different "point" localities (≥0.4 km apart). Although our data set was developed primarily from this subset, we used a few data from the remaining 12 localities for the habitat variables described below. We used this additional data because they were either available with the original records or could be determined independent of accurate mapping.

For each locality, we recorded as many of 12 habitat variables as possible (table 1). For aquatic habitat type, we used the term "stream" for localities with both a well-defined drainage inflow and outflow, whereas we used "pond" for localities lacking a well-defined inflow and little or no outflow. Temporal status of the aquatic habitat was scored as perennial or intermittent based on 7.5' and 15' United States Geological Survey (USGS) topographic maps, but the status of some localities was modified based on field reconnaissance or data provided by other investigators. For many localities, lack of change in the temporal status of the aquatic habitat during the time *R. a. draytonii* was recorded was verified by examining USGS topographic maps bracketing the frog record date(s). We used the designation intermittent to describe the interruption of surface flow in streams or complete dry-down in ponds, either occurring at least once seasonally. Drainage area indicates the size of the hydrographic basin influencing the recorded locality. The drainage area, local gradient, and stream order were largely estimated from 7.5' USGS topographic maps. We estimated large drainage areas (>130 km²) by extrapolation to the recorded locality on topographic maps from either the drainage area for the nearest upstream gauging station (United States Geological Survey 1970a, b) or section counts on United States Forest Service and county maps. Local gradient was estimated from map

Table 1.—Habitat variables recorded for the California red-legged frog *(Rana aurora draytonii)* data set. Subset scored refers to the subset of localities for which we were able to score each variable. Percent scored refers to the percentage of the entire data set (n = 143) for which we were able to score each variable. See text regarding further details concerning the method of data collection for each variable.

	Variable	Subset scored (*n =*)	% scored	Definition
1.	Habitat type	140	98	As (1) stream or (2) pond
2.	Temporal status	137	96	As (1) perennial or (2) intermittent
3.	Drainage area	129	90	In km²
4.	Local gradient	139	97	In angular degrees (°) from horizontal
5.	Water depth	74	52	As (1) presence or (2) absence of water ≥0.7 m deep
6.	Vegetation matrix (emergent or shoreline)	44	31	As (1) dense (area ≥25% thickly vegetated) (2) limited (some, but <25% of area) (3) absent
7.	Native fishes	56	39	As (1) present or (2) absent
8.	Introduced fishes	32	22	As (1) present or (2) absent
9.	Introduced bullfrogs	115	80	As (1) present or (2) absent
10.	Substrate alteration	113	79	As (1) present or (2) absent
11.	Vegetation reduction	106	74	As (1) present or (2) absent
12.	Stream order	127	89	As defined by Strahler (1957)

distances of 0.5-1.0 km across the recorded locality except in the few cases where pronounced local relief required reduction of this distance for an accurate estimate.

Data for the remaining variables (water depth, vegetation matrix, native and introduced fishes, introduced bullfrogs *[Rana catesbeiana]*, substrate alteration, and vegetation reduction) were obtained for subsets of the larger data set from the sources indicated earlier supplemented by Leidy (1984), Moyle and Nichols (1973), Moyle et al. (1982), and Rutter (1908). The exact values used to partition water depth and vegetation matrix variables are arbitrary. However, we chose their general dimensions with the intent of identifying whether the habitat requirements of red-legged frogs suggested by anecdotal data (moderately deep water associated with dense vegetation; see Hayes and Jennings 1986) were supported by this data set. Variation in the collective data set required scoring the fish and introduced bullfrog data as presence/absence, but we also used available data on which fish species were present to interpret the habitat requirements of red-legged frogs. Substrate alteration and vegetation reduction variables indicate alteration of aquatic habitats that was, directly or indirectly, human-effected. We scored substrate alteration as present if evidence existed that the shoreline or substrate topography of the aquatic habitat had been markedly altered (e.g., dams, rip-rap, bank-trampling by cattle). Marked alteration meant that at least 25% of the area of substrate of a locality appeared altered. We scored vegetation as being reduced when data indicated that at least 25% of pre-existing shoreline or emergent vegetation had been removed.

We also gathered current data on a subset of the described localities through field reconnaissance and some information provided by others (data gathered during the interval 1980-1987 represented "current" data). We used these data to help identify temporal changes that may have occurred at sites or in drainage systems for which we had historical data. For this analysis, we used "drainage system" to mean only the primary and highest-order (*fide* Strahler 1957) secondary tributaries of the Sacramento-San Joaquin drainage system. These data were particularly important for indicating where red-legged frogs were probably extinct.

The data set addressing *R. boylii* consists of data published by Moyle (1973) and Moyle and Nichols (1973) from which we re-examined selected elements. Collection methods for these data are thoroughly described therein. Our reanalysis used most of the variables described by Moyle (1973) with some modifications. We used the original estimates of the numbers of each fish species rather than the coded values; the numbers of yellow-legged frogs and bullfrogs remained coded because the original data were recorded as coded. Moyle's stream type variable was reduced to two categories by combining his three intermittent and three perennial stream categories. We also added two variables, one which combines Moyle's cobble and boulder/bedrock substrate categories. The other describes the stream morphology category designated in Moyle's original data as smooth water and fits the definition of a run (Armour et al. 1983). For correlations between yellow-legged frogs and other species, we used only the subset of localities where either or both of yellow-legged frogs and the species being compared was present.

We re-examined these data for four reasons. First, Moyle (1973) summarized data from only some of the sites where yellow-legged frogs were not found. We were equally interested in habitat variation among all sites sampled where yellow-legged frogs had not been found as well as sites where they were found. Second, Moyle (1973) found that the collective abundance of all fish species was inversely correlated with that of yellow-legged frogs, but also commented that yellow-legged frogs were most abundant where native fishes were present. Because original estimates of the numbers of each fish species were available and an inverse relationship between the abundance of native frogs and introduced fishes had already been identified (Hayes and Jennings 1986), we were especially interested in relationships between the abundance of specific native and introduced fishes and that of yellow-legged frogs. Third, Moyle (1973) coded fish abundance when the data, as originally recorded, permit at least ranking, so, where possible, we analyzed the original data directly to minimize bias that can result from coding (Sokal and Rohlf 1981). Lastly, the fish abundance data displayed skewed distributions for several species, so we used non-parametric analyses to avoid having to make any assumptions about sample distributions.

Statistical treatments used are described in Sokal and Rohlf (1981) and Zar (1974). All contingency table comparisons performed had one degree of freedom (df), so all Chi-square values were calculated with the correction for continuity (X^2_c). For those analyses that required more than one comparison using some of the data, alpha (α) was evaluated based on the number of comparisons to a level equivalent to 0.05 using Sidak's multiplicative inequality (Sokal and Rohlf 1981).

RESULTS

California Red-Legged Frog

Rana aurora draytonii was recorded primarily from aquatic habitats that were intermittent streams which included some area with water at least 0.7 meters deep, had a largely intact emergent or shoreline vegetation, and lacked introduced bullfrogs (table 2). We found descriptions adequate to characterize vegetation for 77% (33) of sites where the emergent or shoreline vegetation variable could be scored. With three exceptions, descriptions indicated that either, or both of, an emergent vegetation of cattails (*Typha* spp.) or tules (*Scirpus* spp.), or a shoreline vegetation of willows (*Salix* spp.) were present. Shrubby willows were recorded at 67% (22) of the sites with vegetative descriptions, and were identified as arroyo willow (*Salix lasiolepis*) in the eight instances where a species name was provided. Only juvenile frogs were recorded at five of the six sites where a limited emergent vegetation was present and at the only site that lacked a water depth greater than 0.7 m. We found no significant difference in the numbers of intermittent versus perennial sites with red-legged frogs that had a dense vegetation and a water depth of ≥0.7 m ($X^2_c = 0.338$, $p = 0.561$, for vegetation; $X^2_c = 0.017$, $p = 0.897$, for water depth; $X^2_{df=1,\alpha=0.025} = 5.024$ for both).

Table 3.—Frequency of fish species co-occurrence with *Rana aurora draytonii*. Percentage is the number of sites respective fish species were recorded as a function of all sites where fishes were recorded as co-occurring with *R. a. draytonii*. An asterisk (*) indicates introduced species.

Species	Co-occurrence (n =)	Percentage (%)
California roach *(Lavinia symmetricus)*	19	47
Mosquitofish *(Gambusia affinis)**	10	25
Hitch *(Lavinia exilicauda)*	6	15
Green sunfish *(Lepomis cyanellus)**	6	15
Threespine stickleback *(Gasterosteus aculeatus)*	3	8
Sacramento squawfish *(Ptychocheilus grandis)*	2	5
Sacramento sucker *(Catostomus occidentalis)*	2	5
Prickly sculpin *(Cottus asper)*	1	3
Hardhead *(Mylopharodon conocephalus)*	1	3
Rainbow trout *(Salmo gairdnerii)*	1	3
Brown trout *(Salmo trutta)**	1	3

Table 2.—Variation among habitat variables for California red-legged frogs (Rana aurora draytonii). Number of localities (percentages of localities) in each category are indicated. See table 1 and text for explanation of variable categories.

	Variable	Variable categories		
1.	Aquatic habitat type	(a) stream	129	(92%)
		(b) pond	10	(8%)
2.	Temporal status of aquatic site	(a) perennial	49	(36%)
		(b) intermittent	88	(64%)
3.	Water depth	(a) ≥ 0.7 meters	73	(99%)
		(b) < 0.7 meters	1	(1%)
4.	Emergent and shoreline vegetation	(a) absent	0	(0%)
		(b) limited	9	(20%)
		(c) dense	35	(80%)
5.	Native fishes	(a) present	33	(65%)
		(b) absent	18	(35%)
6.	Introduced fishes	(a) present	14	(44%)
		(b) absent	18	(56%)
7.	Introduced bullfrogs	(a) present	13	(11%)
		(b) absent	102	(89%)
8.	Significant substrate alteration	(a) present	70	(62%)
		(b) absent	43	(38%)
9.	Significant removal vegetation (see #4)	(a) present	1	(2%)
		(b) absent	44	(98%)
10.	Current status (among localities)	(a) probably extant	86	(72%)
		(b) probably extinct	34	(28%)
11.	Current status (among drainages)	(a) probably extant	18	(42%)
		(b) probably extinct	25	(58%)

Rana aurora draytonii was also more frequently recorded at sites with native fishes and with substrate alteration, but less frequently recorded at sites with introduced fishes. Fishes were present at 69% (40 of 58) of sites where data as to their occurrence were recorded; 26 sites had only native fishes, seven had only introduced fishes, and seven had both. Only four fish species, California roach *(Lavinia symmetricus)*, hitch *(Lavinia exilicauda)*, green sunfish *(Lepomis cyanellus)*, and mosquitofish *(Gambusia affinis)*, were recorded as co-occurring with *R. a. draytonii* at more than three sites (table 3), and only California roach was recorded at more than 25% (10) of sites. Sixty of the 70 sites described as being substrate-altered at the time *R. a. draytonii* was recorded were small impoundments.

California red-legged frogs were also most frequently recorded at sites influenced by a small drainage area, having a low local gradient, and in streams having a low stream order. Drainage areas of sites from which *R. a. draytonii* was recorded vary from 0.02 km^2 to over 9000 km^2, but twothirds (n = 83) are from localities with drainage areas ≤40 km² (fig. 1). Local gradient (slope) at California red-legged frog localities varies from 0.04° to 12.8° from horizontal, although 87% (n = 100) occur at sites with slopes ≤2°. California red-legged frogs have been recorded in 1st to 6th order streams, but 94% (n = 119) of these localities are 4th- or lesser-order streams and 42% are 1st-order streams (fig. 2).

Based on the subset for which current data were available (n = 120), California red-legged frogs are probably extinct at >25% of the localities where they were historically recorded. When clustered into a sample representing drainage systems (n = 43; see methods), this subset indicates that California red-legged frogs are probably extinct in over 50% of the drainage systems in the Central Valley area. Three habitat variables (temporal status of aquatic habitat, drainage area, and introduced bullfrogs) showed a significant relationship to the probability of survival of local populations of California red-legged frogs (table 4). We found that *R. a. draytonii* is likely extant at 82% (n = 70) of localities with an intermittent aquatic habitat, whereas it is probably extinct at 71% (n = 22) of the sites with a perennial aquatic habitat. Grouping localities based on drainage area, *R. a. draytonii* is probably extant at 83% (n = 85) of sites influenced by a small (<300 km²) drainage area, whereas it is probably extinct at all recorded localities (n = 11) influenced by a large (≥300 km²) drainage area. Moreover, available data indicate that *R. a. draytonii* is extinct at all recorded localities on the Central Valley floor, which includes all localities affected by the largest drainage areas (n = 10). Similarly, *R. a. draytonii* is probably extant at 81% (n = 70) of localities lacking introduced bullfrogs and is probably extinct at all localities (n = 10) where it has been recorded with bullfrogs. Remaining variables either failed to show a significant relationship to the probability of California red-legged frog survival (table 4), or one of the variable categories was so rare that this analysis was not applicable (see table 2).

Table 4.—Contingency analysis relating selected habitat variables to an estimate of the likelihood that historically recorded California red-legged frog populations are extant. Status of frog populations at recorded localities are indicated as extant (= probably extant) and extinct (= probably extinct). A double asterisk (**) denotes significant contingency tables, based a critical $X^2_{df=1,\alpha(2)=0.007}$ = 7.3, α adjusted for seven comparisons (see methods).

	Variable	Condition	Locality Status extant	Locality Status extinct	X^2_c	Probability
1.	Temporal status	Perennial	9	22	27.326	0.0001**
		Intermittent	70	15		
2.	Drainage area	≥300 km²	0	11	31.466	0.0001**
		<300 km²	85	18		
3.	Native fishes	+	13	6	0.276	0.5991
		-	14	11		
4	Introduced bullfrogs	+	0	10	27.140	0.0001**
		-	70	16		
5.	Substrate alteration[a]	+	25	14	0.983	0.3215
		-	47	14		
6.	Introduced fishes	+	5	9	0.003	0.9524
		-	7	10		
7.	Substrate alteration[b]	+	21	3	<0.001	0.9944
		-	26	5		

[a]*Analysis with all localities.*

[b]*Analysis with subset of localities having a drainage area ≤25 km².*

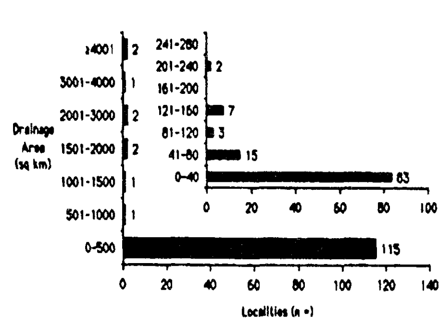

Figure 1.—Frequency distribution of localities where *Rana aurora draytonii* has been recorded in the Central Valley, California based on drainage area. The inset details the frequency distribution of localities with drainage areas < 280 km².

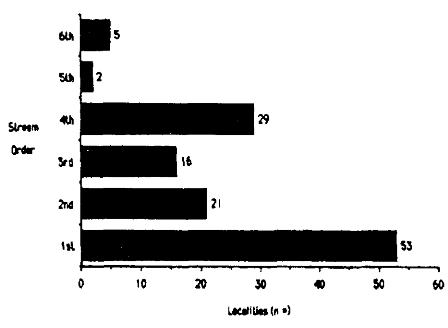

Figure 2.—Frequency distribution of localities where *Rana aurora draytonii* has been recorded in the Central Valley, California based on stream order.

Foothill Yellow-Legged Frog

Rana boylii was recorded primarily from shallow, partly shaded stream sites with riffles and at least a cobble-sized substrate. All 29 stream sites at which either post-metamorphic or larval *R. boylii* were recorded were ≤0.6 m in average water depth (fig. 3) and had at least some shading (fig. 4). *Rana boylii* was recorded more frequently at sites with a stream area that was >20% shaded than at sites with ≥20% shading. Only one of 29 *R. boylii* sites lacked riffle habitat and *R. boylii* was recorded significantly more frequently at sites with >40% riffle area than at sites with a riffle area of ≤40% [$X^2_c = 8.680$, p = 0.003, $X^2_{df=1,\alpha(2)=0.025} = 5.024$; fig. 5]. Only four of 29 *R. boylii* sites lacked at least a cobble-sized substrate and *R. boylii* was recorded most frequently (20 of 29) at sites with >40% of the substrate that was at least cobble-sized (fig. 6). Few other patterns could be identified from among the environmental variables that we re-analyzed. *Rana boylii* was recorded more frequently from perennial streams (n = 19) than from intermittent ones (n = 10), but the difference was not significant when compared to the total number of perennial (n = 71) and intermittent (n = 59) stream sites sampled [$X^{2c} = 1.268$, p = 0.260, $X^2_{df=1,\alpha(2)=0.025} = 5.024$]. Of 13 environmental variables that we re-examined, only the percentage of stream area in riffles was significantly correlated with the abundance of *R. boylii* (table 5).

Rana boylii occurred with 1-5 ($\bar{x}$ = 2.5) of the vertebrate members of the aquatic macrofauna at 26 of the 29 localities where it was recorded.

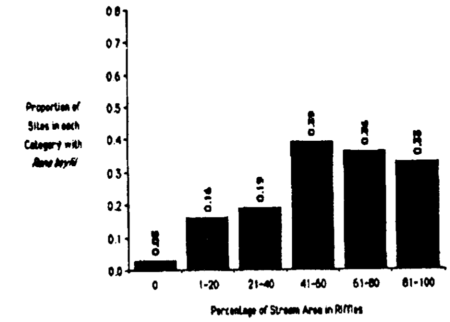

Figure 5.—Histogram of the proportion of sites in riffle categories where *Rana boylii* has been recorded in the Sierra Nevada foothills, California. Sample sizes as a function of the total sample in each riffle category are: 0% (n=1/36), 1-20% (n=5/31), 21-40% (n=4/21), 41-60% (n=11/28), 61-80% (n=7/19), and 81-100% (n=2/6).

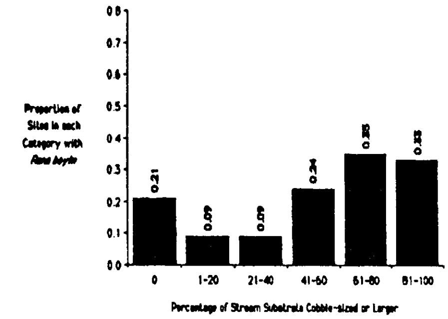

Figure 6.—Histogram of the proportion of sites in substrate categories where *Rana boylii* has been recorded in the Sierra Nevada foothills, California. Sample sizes as a function of the total sample in each substrate category are: 0% (n=4/19), 1-20% (n=3/32), 21-40% (n=2/23), 41-60% (n=7/29), 61-80% (n=9/26), and 81-100% (n=4/12).

Foothill yellow-legged frogs were recorded as occurring with 12 different species, but co-occurrence, expressed as the percentage of total sites at which either *R. boylii* or the co-occurring species were recorded, did not exceed 31% (table 6). Introduced species (n = 6) occurred with *R. boylii* less frequently ($\bar{x}$ = 2, 1-3) than native species ($\bar{x}$ = 9.3, 1-17) and native species had a significantly higher percentage of co-occurrence (3-31%, $\bar{x}$ = 16.5%) than introduced species [n = 6; 2-9%, $\bar{x}$ = 3.7%; Mann-Whitney test, U′ = 32.5, p = 0.0275, $U_{critical,\alpha(2)=0.05} = 31$]. Only four native fishes, California roach, Sacramento sucker *(Catostomus occidentalis)*, Sacramento squawfish *(Ptychocheilus grandis)*, and rainbow trout *(Salmo gairdnerii)*, occurred with *R. boylii* at more than three of the 29 sites where the latter was recorded, and of these, only California roach occurred with *R. boylii* at more than 50% of the sites where *R. boylii* was recorded. Only one species assemblage, that consisting of California roach, Sacramento squawfish, and Sacramento sucker, occurred with *R. boylii* more often than expected by chance alone (table 7). Correlation analysis indicated that the abundance of 10 of the 12 co-occurring species was significantly inversely correlated with the abundance of *R. boylii* (table 8).

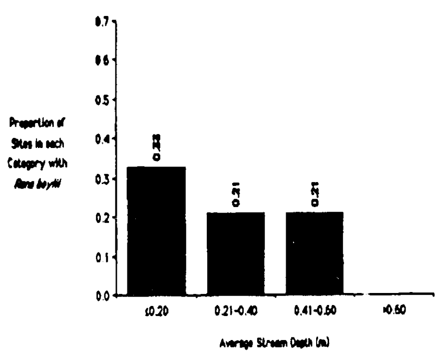

Figure 3.—Histogram of the proportion of sites in stream depth categories where *Rana boylii* has been recorded in the Sierra Nevada foothills, California. Sample sizes as a function of the total sample in each stream depth category are: <0.20 (n=8/24), 0.21=0.40 (n=9/43), 0.41-0.60 (n=12/57), and >0.60 (n=0/18).

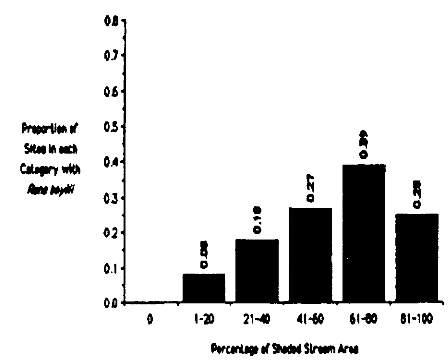

Figure 4.—Histogram of the proportion of sites in stream shading categories where *Rana boylii* has been recorded in the Sierra Nevada foothills, California. Sample sizes as a function of the total sample in each stream shading category are: 0% (n=0/5), 1-20% (n=3/37), 21-40% (n=7/38), 41-60% (n=8/30), 61-80% (n=9/23), and 81-100% (n=2/8).

DISCUSSION

Habitat Variation

California Red-Legged Frog

A dense vegetation close to water level and shading water of moderate depth are habitat features that appear especially important to California red-legged frogs. Previous authors have suggested or implied the occurrence of at least one of these habitat features. Storer (1925) noted that *R. a. draytonii* in streams was restricted to large pools, which implies a moderate water depth. Stebbins (1966, 1985) emphasized vegetative cover as important to red-legged frogs, but his comments confound habitat characteristics that may be attributable to northern versus California (southern) red-legged frogs; data on these two forms should remain partitioned until it is well-established that they are not different species (Hayes and Miyamoto 1984, Hayes and Krempels 1986). Zweifel (1955) coupled the water depth and vegetation features of California red-legged frog habitat, but he emphasizes a herbaceous shoreline vegetation. Our data indicate that a more complex vegetation is a feature of sites where *R. a. draytonii* occurs. Cattails, bulrushes, and shrubby wil-

Table 5.—Spearman rank correlation between selected environmental variables and the coded abundance of *R. boylii* as measured by Moyle (1973). Sample size for each variable is n = 130. A double asterisk (**) indicates significant correlations, based on a critical $r_s = 0.267$ at an α(two-tailed) = 0.002, adjusted for 24 comparisons (13 below and 11 in table 8; see methods).

Variable	Correlation coefficient (r_s =)
Human alteration	-0.160
Vegetation	
Aquatic vegetation (%)	-0.157
Floating vegetation (%)	-0.169
Shade (%)	0.219
Stream morphology	
Pools (%)	-0.205
Riffles (%)	0.304**
Runs (%)	-0.020
Stream substrate	
Mud (%)	-0.035
Sand (%)	-0.085
Gravel (%)	-0.032
Rubble (%)	0.071
Boulder/Bedrock (%)	0.192
Rubble/Boulder/Bedrock (%)	0.172

Table 6.—Occurrences of aquatic macrofaunal species among the 130 stream sites sampled by Moyle (1973) and Moyle and Nichols (1973). Co-occurrences is the number of sites *Rana boylii* was found to co-occur with each species. Percentage of co-occurrences is co-occurrences as the percentage of those sites at which either *R. boylii* or the state species occur. An asterisk (*) indicates introduced species. Ten other fish species (Goldfish *(Carassius auratus)*, Prickly sculpin *(Cottus asper)*, Common carp *(Cyprinus carpio)*, Threadfin shad *(Dorosoma petenense)*, Threespine stickleback *(Gasterosteus aculeatus)*, Yellow bullhead *(Ictalurus nebulosus)*, Redear sunfish *(Lepomis microlophus)*, Chinook salmon *(Onchorhynchus tshawytscha)*, Brown trout *(Salmo trutta)*) were recorded at low numbers of stations ($\leq$8); none were recorded as co-occurring with *R. boylii*.

Species	Occurrences (n =)	Co-occurrences (n =)	% of co-occurrences
Bullfrog *(Rana catesbeiana)**	68	2	2
Green sunfish *(Lepomis cyanellus)**	61	2	2
Sacramento sucker *(Catostomus occidentalis)*	55	13	18
Sacramento squawfish *(Ptychocheilus grandis)*	48	12	18
California roach *(Lavinia symmetricus)*	43	17	31
Largemouth bass *(Micropterus salmoides)**	41	0	0
Mosquitofish *(Gambusia affinis)**	37	1	2
Bluegill *(Lepomis macrochirus)**	33	3	5
Rainbow trout *(Salmo gairdnerii)*	27	11	24
White catfish *(Ictalutus catus)**	13	1	2
Golden shiner *(Notemigonus crysoleucas)**	13	0	0
Hitch *(Lavinia exilicauda)*	12	1	3
Hardhead *(Mylopharodon conocephalus)*	11	2	5
Smallmouth bass *(Micropterus dolomieui)**	9	3	9

Table 7.—Frequencies of species assemblages of aquatic macrofaunal vertebrates co-occurring with *R. boylii* from data recorded by Moyle (1973). Assemblages listed include only combinations of species recorded as co-occurring with *R. boylii* at least seven localities (see table 6). Listed species are California roach (RCH), Sacramento sucker (SKR), Sacramento squawfish (SQ), and Rainbow trout (RT). Asterisks (**) identify assemblages co-occurring at frequencies significantly higher than expected by chance, based on a critical $X^2_{df=1,\alpha=0.005} = 7.879$, adjusted for 11 combinations (see methods). Probabilities (p) are those associated with calculated X^2_c values.

Species assemblage	Frequencies: Observed	Frequencies: Expected	X^2_c	Probability
RCH/RT/SKR/SQ	2	1.20	0.077	0.75<p<0.90
RCH/SKR/SQ	9	3.15	9.068**	0.003
RCH/RT/SQ	2	2.67	0.011	0.90<p<0.95
RCH/RT/SKR	2	2.89	0.053	0.75<p<0.90
RT/SQ/SKR	2	2.04	0.104	0.50<p<0.75
RCH/RT	5	6.45	0.139	0.50<p<0.75
RCH/SKR	10	7.62	0.463	0.25<p<0.50
RCH/SQ	9	7.03	0.305	0.50<p<0.75
RT/SKR	3	4.93	0.415	0.50<p<0.75
RT/SQ	3	4.55	0.243	0.50<p<0.75
SKR/SQ	11	5.38	4.959	0.026

lows, the plants comprising emergent and shoreline vegetation at such sites, typically shade a substantial surface area of water with a dense matrix at or near water level. California red-legged frogs appear sensitive to the presence of such a vegetation structure because most sites from which frogs were recorded lacked significant alteration of emergent or shoreline vegetation (see table 2). Moreover, because only juvenile frogs were recorded from most sites with limited shoreline or emergent vegetation, a minimum amount of such vegetation appears to be needed for survival of adults. Parallel arguments apply to water depth. Previous authors have characterized *R. a. draytonii* as a pool- or pond-dwelling species (Stebbins 1966, 1985; Storer 1925; Zweifel 1955) and descriptions corresponding to that characterization were recorded for this frog at most sites. Yet, we found that using minimum water depth was a more encompassing habitat descriptor because it included canals and stream sites where adult frogs were described as being common and that had the minimum water depth requirement, but could not be described as either ponds or stream pools. Available description of such sites indicates that they fit the definition of a run (Armour et al. 1983), although data upon which part of the definition is based (the rate of water flow) are lacking.

We believe that California red-legged frogs occur primarily in streams because alternative sites (ponds) that have suitable water depth and vegetation characteristics were historically rare outside of stream habitats rather than because red-legged frogs are somehow preadapted for survival in streams. Historically, pond habitats below 1500 m in the Central Valley were mostly vernal pools, a habitat too shallow and ephemeral to develop the macrovegetation found associated with *R. a. draytonii* (see Holland 1973, Jain 1976). Even the only two exceptions to *R. a. draytonii* not occurring in vernal pools support this hypothesis. A large vernal pool in San Obispo County, California is known to have a population of California red-legged frogs (D. C. Holland, pers. comm.). However, this vernal pool is atypical because it possesses significant macrovegetation and water depth. These features appear to be present because this large (ca. 20 ha) pool does not dry down each year. The second exception is a vernal pool in coastal southern California in which two frogs with abnormal numbers of legs were found (Cunningham 1955). Cunningham thought that the defects were induced by exposure to high temperatures during early development, a condition facilitated by the limited vegetative cover that was present. His speculation may be valid if California red-legged frog embryos have a low critical thermal maximum (Hayes and Jennings 1986). Storer (1925) thought that *R. a. draytonii* was excluded from temporary (vernal) pools because its larval period is relatively long, but the more likely mechanism is that frogs immigrating to such pools were unable to establish because suitable habitat was lacking. The latter hypothesis is supported because California red-legged frogs are not recorded from the many vernal pools that hold water for intervals longer than the minimum time required by *R. a. draytonii* to complete metamorphosis (10 weeks; Hayes, unpubl. data; see also Jain 1976, Zedler 1987).

Rana a. draytonii also appears to have responded to the creation of habitat with the appropriate vegetation and water depth characteristics. A significant aspect of the changes in aquatic habitats that have occurred in the Central Valley below 1500 m is an increase in the number of permanent ponds (Moyle 1973). Storer (1925) reported that *R. a. draytonii* occurred in a number of water storage reservoirs and artificial ponds, but the habitat features of those sites

Table 8.—Spearman rank correlation between the numerical (non-coded) abundance of the vertebrate macrofauna and the abundance (coded) of *R. boylii* as recorded by Moyle (1973). Sample size is based on the total number of sites where either *R. boylii* or the species being compared was present. A single asterisk (*) indicates introduced species. A double asterisk (**) identifies significant correlations at an _ (two-tailed) = 0.002, adjusted for 24 comparisons (11 below and 13 in table 5; see methods). Probability (p) is the probability of obtaining the calculated Spearman correlation coefficient (r_s). Common names for the listed species are in table 6.

Species	Sample size (*n* =)	Correlation coefficient (r_s =)	Probability (*p* =)	Critical r_s
Catostomus occidentalis	71	-0.404**	<0.001	-0.363
*Gambusia affinis**	62	-0.835**	<0.001	-0.388
*Ictalurus catus**	41	-0.798**	<0.001	-0.473
Lavinia exilicauda	40	-0.760**	<0.001	-0.479
Lavinia symmetricus	55	-0.316	0.020	-0.411
*Lepomis cyanellus**	88	-0.742**	<0.001	-0.327
*Lepomis macrochirus**	59	-0.827**	<0.001	-0.397
*Micropterus dolomieui**	35	-0.538**	0.001	-0.510
Mylopharodon conocephalus	38	-0.607**	<0.001	-0.491
Ptychocheilus grandis	66	-0.541**	<0.001	-0.376
*Rana catesbeiana**	90	-0.800**	<0.001	-0.323
Salmo gairdnerii	44	-0.425	0.005	-0.458

were not described. Thus, it was of special interest to find that no significant difference could be identified between the probability of extinction of *R. a. draytonii* at substrate-altered sites (mostly small impoundments) and at sites lacking such alteration. Moyle (1973) concluded that the decline of *R. a. draytonii* was related in part to human-induced alteration, including creation of impoundments. Our data suggest that human-induced alteration creating small impoundments cannot be related directly to the disappearance of California red-legged frogs. We emphasize that these data do not exclude the alternative, discussed later, which indicates that the creation of small impoundments is likely to have an indirect negative effect on *R. a. draytonii* by facilitating the dispersal of introduced aquatic predators.

Besides features of habitat structure associated with *R. a. draytonii*, its isolation from one or more aquatic macrofaunal predators is the other key element suggested by these data. No significant variation was found in the features of habitat structure important to *R. a. draytonii* between intermittent and perennial aquatic sites, so differences in habitat structure cannot explain why *R. a. draytonii* is recorded most frequently from intermittent aquatic sites. We believe that California red-legged frogs were recorded most frequently from intermittent sites because the likelihood of extinction at perennial sites is now higher than at intermittent sites (see table 4) and few historical data are available from when frogs were often found at perennial sites.

California red-legged frogs are now extinct from all sites on the Central Valley floor, all of which were perennial and, except for one, were recorded prior to 1950. We believe that the disadvantage associated with perennial sites and the advantage associated with intermittent sites is the degree to which the former allow, and the latter restrict, the access of aquatic macrofaunal predators.

The remaining variation in features of *R. a. draytonii* habitat we have identified can be directly, or indirectly, linked to a hypothesis invoking the influence of one or more aquatic macrofaunal predators. The significantly lower likelihood of extinction at sites with small drainage areas (table 4) and *R. a. draytonii* being recorded from a greater number of localities with smaller drainage areas (fig. 1) and lower stream orders (fig. 2), are probably unrelated to either drainage area or stream order effects per se. Rather, they are a function of both the bias against recording historical data and the fact that sites with smaller drainages or lower stream orders have a higher probability of being intermittent aquatic habitats, which have a higher probability of excluding aquatic predators. Limited co-occurrence with aquatic predators, namely bullfrogs and predatory fishes, and a significantly higher likelihood of extinction at sites where bullfrogs were recorded (table 4) may indicate a negative interaction with one or more of these species. *Rana a. draytonii* did not co-occur with any fish species frequently. It co-occurred most often with California roach, a small, omnivorous native fish that is thought to have declined, in part, due to predation by introduced fishes (Moyle and Nichols 1974, Moyle 1976). We did not detect a significantly higher likelihood of extinction at sites with introduced fishes. However, the sample was too small to partition to permit testing individual fish species, the level at which we believe such an effect is most likely.

While we are reasonably convinced that the greater restriction of *R. a. draytonii* to intermittent aquatic habitats is an effect due to novel aquatic predators, we emphasize that these data cannot identify which are the aquatic predators producing such an effect. The inability to identify the responsible predators is complicated by the condition of limited overlap between each potential predator and *R. a. draytonii*. That condition prevents excluding the alternative that different habitat requirements rather than any predatory interaction may explain the limited overlap in habitat use between each putative predator and California red-legged frogs (compare Moyle 1973 for bullfrogs and Moyle and Nichols (1973) for various fishes, but especially mosquitofish and green sunfish; see also Hayes and Jennings 1986 for a discussion). It is this fact and the apparent intolerance of *R. a. draytonii* to unshaded habitat that leads us to suggest that some alteration of riparian vegetation may be necessary to create the conditions for a negative interaction.

Foothill Yellow-Legged Frog

Partly shaded, shallow streams and riffles with a rocky substrate that is at least cobble-sized are the habitat features that appear to be important to foothill yellow-legged frogs. Previous authors agree that *R. boylii* occurs in streams (Moyle 1973; Stebbins 1966, 1985; Storer 1925; Zweifel 1955), but variation exists in the features of streams associated with these frogs. Of environmental variables that appear important to *R. boylii*, the percentage of stream area in riffles is the only one we were able to correlate significantly, albeit weakly, with its abundance. Moyle (1973) obtained a similar positive correlation in his original analysis of the same data, and Stebbins (1966, 1985) also emphasized riffles as one of the key aspects of *R. boylii* habitat. The reason for the weak correlation we found is uncertain, but one or more of three factors probably produced that result. First, as intermittent streams lose surface flow during late summer, riffles disappear, and *R. boylii* can then be found associated with stream pools (Fitch 1938, Slevin 1928, Storer 1925, Zweifel 1955).

Moyle's data were collected in late summer and 10 of the 29 stream sites at which *R. boylii* was recorded were intermittent, so data from these sites may have diluted the correlation. Second, riffle area may be correlated with the abundance of *R. boylii* only above or below certain values (see fig. 5). Lastly, *R. boylii* has been reported from sites with little or no riffle habitat unrelated to seasonal patterns (Fitch 1938, Zweifel 1955).

Apart from riffles, our reanalysis of environmental variables differs from that of Moyle (1973), who found that five of the other variables that we re-examined were either positively (i.e., shading and boulder/bedrock; compare table 1 in Moyle [1973] and our table 5) or negatively (i.e., rooted vegetation [= our aquatic vegetation], pools, man modified [= our human alteration]) significantly correlated with the abundance of *R. boylii*. We attribute this difference, in part, to our analysis being more conservative because we adjusted α for the experimentwise error rate, our analysis was not restricted to localities where only frogs were found, and we used non-parametric tests. Some of the correlations that Moyle (1973) observed with *R. boylii* abundance may have been significant due to one or more of these differences. We must emphasize, however, that several of the variables that Moyle found correlated with *R. boylii* abundance vary differentially in their occurrence between riffles and pools (e.g., boulder/bedrock; see Moyle [1973] and Moyle and Nichols [1973]). Those variables are also susceptible to the seasonal correlation-altering effects discussed for the riffle variable. Thus, a conservative analysis, like ours, is less likely to detect variables related to frog abundance within such a data set.

Nevertheless, variables identified as important to *R. boylii* need not be correlated to its abundance. Stream depth, shading, and substrate type may represent such variables. Our reanalysis of Moyle's data suggests that sites with a shallow average stream depth are somehow advantageous (see fig. 3). Moyle (1973) found no significant correlation between the abundance of *R. boylii* and stream depth, and he did not discuss stream depth with respect to foothill yellow-legged frogs in any other context. Zweifel (1955) noted that streams in which *R. boylii* occurred were seldom more than 0.3 m deep, and Fitch (1936), Storer (1925), and Wright and Wright (1949) found that *R. boylii* usually lays eggs in shallow water. Still, overall importance of stream depth to *R. boylii* remains unclear. Our reanalysis also suggests that some advantage is linked to increased shade up to some intermediate level (see fig. 4). Zweifel (1955) described shading in typical *R. boylii* habitat as interrupted, whereas Moyle (1973) reported a positive correlation between frog abundance and the degree of shading.

Some workers have emphasized the degree of openness or insolation in *R. boylii* habitat, rather than addressing shading (Fitch 1938; Stebbins 1966, 1985). Nevertheless, even the latter imply that some shading is present. Fitch's (1938) suggestion that yellow-legged frogs are excluded by dense canopy may be supported by Moyle's data because he recorded no *R. boylii* at sites with >90% shading (see also fig. 4). Our reanalysis also suggests that some advantage is associated with sites possessing at least a cobble-sized substrate (see fig. 6). Although workers have most frequently emphasized the rocky aspect of *R. boylii* habitat (Fitch 1936, 1938; Moyle 1973; Stebbins 1966, 1985; Storer 1925), substrate descriptions of that habitat are probably as varied as any other single variable. Moyle (1973) identified a positive correlation between the percentage of stream area with bedrock and boulders and the abundance of *R. boylii*, yet sites with gravely (Gordon 1939), sandy (Zweifel 1955), or muddy substrates have also been recorded (Fitch 1938, Storer 1925). Because Moyle's data do not provide frog age, we could not determine whether sites having a substrate that was less than cobble-sized were simply marginal habitat with juvenile *R. boylii* (see Zweifel 1955), or whether they represented real variation in habitat used by established populations.

Fitch (1938) and Zweifel (1955) reported on a few sites with adult frogs that lacked a substrate that was cobble-sized or larger and appeared to have few predators. They suggested that yellow-legged frogs are rarely recorded from such sites because their predators may access the "atypical" habitat more easily. Nevertheless, data on the aforementioned variables reinforce the conclusion already arrived at with *R. a. draytonii*: Existing data cannot distinguish hypotheses explaining the differential occurrence of *R. boylii* among habitat categories due to mechanistic or physiological restriction (i.e., "habitat preference") from hypotheses invoking habitat restriction because of some novel predator (Hayes and Jennings 1986). The data for *R. boylii* differ from that of *R. a. draytonii* in that we cannot confidently reject the alternative that no restriction is occurring. For example, it remains unclear whether earlier reports of "atypical" habitat use by *R. boylii* were simply rare occurrences, or whether those instances actually reflect a general pattern of broader habitat use in years prior to when Moyle (1973) obtained his data, indicating that habitat restriction had occurred.

Management Implications

Both *R. a. draytonii* and *R. boylii* need immediate management consideration if many remaining populations are to survive into the next century. *Rana a. draytonii* is extinct on the floor of the Central Valley, and is probably extinct from over half of the drainage systems in the Central Valley from where it was historically recorded. We consider many of the remaining populations at risk since over half of the localities are within areas projected to be flooded by reservoirs proposed for the Coast Range slope of the Central Valley (Wernette et al. 1980; C. J. Brown, Jr., pers. comm.). Populations at an additional 10 localities are at an unknown, but probably high level of risk. Although these additional localities will not be flooded by the proposed reservoirs, flooding will isolate the frogs present in small (<10 km^2) drainage basins upstream of the reservoirs. We lack data on how isolation in very small drainage basins may increase the probability of extinction (see Fritz 1979), but the only four localities isolated by reservoirs for which data exist now lack red-legged frogs (Hayes, unpubl. data). California red-legged frogs were recorded at each of the latter sites up to 20 years ago, between one and five years after flooding of the adjacent reservoir had taken place. Comparable data on the decline of *R. boylii* in the Central Valley are lacking, but observations by experienced workers indicate that *R. boylii* no longer occurs at many localities in the Central Valley drainage basin where it was historically recorded (Moyle 1973; R. Hansen, D. Holland, S. Sweet, D. Wake, pers. comm.; Jennings, unpubl. data).

Modal habitat requirements for both frog species suggested by existing data should be given special attention in any management attempt. Since our comments here are based on data for both species in the Central Valley of California, attempts to apply the management recommendations we make to other areas within the geographic range of each species should be done cautiously. We cannot overemphasize that preservation of what appears to be the preferred (modal) habitat condition for either species should be stressed where it is ambiguous whether restriction is due either to the negative impact of the introduced aquatic macrofauna, or to intrinsic mechanical or physiological limitations. Preservation of non-modal habitat is not only likely to incur a greater cost to ensure frog survival, but more importantly, it may still not allow survival if the worst-case scenario (restriction of habitat by the introduced aquatic macrofauna) is true.

The modal habitat features of *R. a. draytonii* and *R. boylii* are similar in two ways. First, the aquatic habitat of each has some shading. Yet, shading associated with California red-legged frogs differs because of the apparently crucial aspect of having dense vegetation at or near water level. We lack details on just how the streams Moyle (1973) sampled were shaded, but knowledge of some of the species providing shade suggests that a higher overstory was typical. *Rana a. draytonii* will always be at greater risk than *R. boylii* where alteration of riparian vegetation is a problem simply because of its shade requirement; even altered stream environments may retain some shading, but a lesser probability will always exist that the shading that remains will have the structure needed by *R. a. draytonii*. Second, each species occurs most frequently in the absence of any aquatic macrofauna, and both species have probably experienced some habitat restriction due to introduced aquatic predators. Only one small native minnow cooccurs at over one-third the sites where each frog species was recorded, and even that species was not positively correlated with frog abundance. For *R. a. draytonii*, the data are reasonably convincing that restriction has occurred away from perennial aquatic sites, For *R. boylii*, data do not clearly indicate habitat restriction. Still, the fact that *R. boylii* was found at fewer intermittent sites leads us to believe that if habitat restriction has taken place, it has occurred away from intermittent aquatic sites. We reason that since riffles disappear seasonally in intermittent streams, such streams lack the condition found in perennial streams that may be an advantage if riffle habitat is a refuge, i.e., that perennial streams have riffle habitat year-round.

Our analysis indicates that attempts at management of these two frogs should address at least three other habitat variables: water depth, stream morphology, and substrate type. *Rana boylii* appears to require a shallow water depth of <0.6 m, whereas *R. a. draytonii* seems to require some water _0.7 m deep. Data on stream morphology and substrate type, which were recorded only for *R. boylii*, suggest that both of a percentage of riffle area and at least cobble-sized substrate of greater than 40% best suit this species. Parallel data for *R. a. draytonii* are lacking, but since data on other habitat parameters measured for *R. a. draytonii* are largely "reciprocals" of the correlates of riffle habitat associated with *R. boylii*, we anticipate that some relationship to the more lentic water stream morphology categories (i.e., pools and runs) and their associated finer substrate categories (i.e., silt and sand) will be demonstrated for *R. a. draytonii*.

Experiments may ultimately identify the introduced aquatic predators likely responsible for the declines of these frogs, but management based on current knowledge should address no less than the worst-case scenario; i.e., that any member of the introduced aquatic macrofauna presents a risk to the survival of populations of *R. a. draytonii* and *R. boylii*. Thus, the sound management decision is to implement measures that will maximize the degree of isolation between existing populations of each frog species and any members of the introduced aquatic macrofauna. Just how isolation should be maintained will vary depending on the site considered, but some general suggestions can be made. First, passive measures promoting isolation are preferable because they are less costly and are less likely to affect non-target species. Simply avoiding habitat modification where the modal habitat features for each frog species already exist is a passive measure that will provide some degree of within-habitat isolation since members of the introduced aquatic macrofauna show little overlap in their habitat requirements with each frog. Yet, populations of either frog species currently coexisting in a habitat mosaic with members of the introduced aquatic macrofauna may still be doomed. This possibility leads us to suggest that most efforts at management should be spent on frog populations at sites that currently lack introduced aquatic predators. We consider protection of the entire hydrographic basins of drainage systems tributaries (see methods for definition) an important part of such management attempts because intrusion by introduced aquatic predators is probably most easily controlled if the only natural access route is via upstream movement. To our knowledge, no locality within the Central Valley drainage area having an extant California red-legged frog population has its entire hydrographic basin protected. Moreover, only two California red-legged frog populations within this area occur at sites where the habitat is currently offered some protection. Second, isolation strategies may differ depending on whether proximate populations of introduced aquatic predators are bullfrogs or fishes or both. Apart from being physically transported, fishes are effectively prevented from moving upstream by a barrier (see Hayes and Jennings 1986), whereas bullfrogs, capable of overland movement under wet conditions (Hayes and Warner 1985), are less likely to be barrier-limited. We indicated earlier that creation of small impoundments may enhance the ability of *R. a. draytonii* to establish at certain sites through the creation of features found in its habitat, but attention to the positioning of such impoundments is an equally important consideration. If impoundments are close enough that bullfrogs reach them from an adjacent source population, such sites can also act as local refuges at which new bullfrog populations can become established, and can serve as new focal points from which to disperse. Moreover, new impoundments probably favor the establishment of bullfrogs simply because their unvegetated condition more closely matches the habitat recorded for bullfrogs (Moyle 1973). These arguments simply indicate that particular attention should be given to avoiding the creation of "stepping-stone" pathways, i.e., provision of access into currently isolated drainages by the positioning of impoundments that permit introduced predators, like bullfrogs, to encroach progressively by dispersal.

The limits of our analysis indicate that significant aspects of habitat variation for both frog species remain to be understood. In particular, an understanding is needed as to how key variables influence reproduction and refuge sites. Although available data on oviposition patterns suggest a link between *R. a. draytonii* and the presence of emergent vegetation (Hayes and Miyamoto 1984), and *R. boylii* and a rocky substrate (Fitch 1936, 1938; Storer 1925; Zweifel 1955), it is unclear for either species to what degree the substrate can vary before oviposition may be prevented and also how aspects of reproduction besides oviposition may be linked to habitat variation. Perhaps the most crucial gap is a lack of understanding of what aspects of habitat variation are related to frog refuge sites, including the often temporary refuges used as an escape from predators as well as those refuges used during the season of inactivity. The former type of refuge site may be related to the deep-water and dense vegetation habitat associated with *R. a. draytonii*, and the riffle habitat associated with *R. boylii*, but what aspects of those habitat features really comprise the refuge and to what degree they may vary before they are no longer a refuge is unknown. A understanding of the latter is pivotal to the identification of predator-induced habitat restriction. Most importantly, an understanding of how reproduction and refuge sites are related to habitat variation for these two frogs is essential if management is to ever be refined to a level where habitat variables, either individually or in concert, may be manipulated. Finally, if habitat manipulations are attempted, they will have to be implemented with caution in aquatic systems where both *R. a. draytonii* and *R. boylii* co-occur; differences in habitat characteristics between each species suggest that whatever way one or more of several habitat variables are manipulated, they will probably result in a tradeoff between habitat losses and habitat gains for *R. a. draytonii* versus *R. boylii*.

In summary, habitat analysis for the two ranid frogs, *R. a. draytonii* and *R. boylii*, indicates that each species is most frequently associated with discernibly different aquatic habitats, the former with densely vegetated, deep water and the latter with rocky, shallow-water riffles in streams. The species are similar in that they infrequently co-occur with any aquatic vertebrates, especially the introduced aquatic macrofauna. Low levels of co-occurrence between frogs and the introduced aquatic macrofauna have two confounded explanations: 1) preferential use of different habitats between the introduced aquatic macrofauna and frogs, and 2) habitat restriction because frogs and their life stages are preyed upon by the introduced aquatic macrofauna. However, even though it is presently impossible to identify the responsible predator, temporal data strongly suggest that *R. a. draytonii* has been restricted by some introduced aquatic predator and the same possibility cannot be excluded for *R. boylii*. For both species, a management scheme is necessary to avert existing trends of decline, and ultimately, extinction. A management scheme that minimizes the risk of extinction based on current data must address the worst-case scenario among the alternatives implicated in limiting frog distributions. To address anything less increases the risk of extinction if that alternative is true. Since that alternative is habitat restriction by an introduced aquatic macrofauna, management should strive to isolate both frog species from the introduced aquatic macrofauna. Moreover, available data indicate that preservation of modal conditions for habitat variables identified as associated with each species is a suitable interim strategy, since it is more likely to promote isolation. Significant refinements of this management scheme will require a thorough understanding of how habitat variables associated with each frog species are linked to their refuge requirements and their reproductive patterns.

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