
COMPARATIVE MICROHABITAT CHARACTERISTICS AT OVIPOSITION SITES OF THE CALIFORNIA RED-LEGGED FROG (*RANA DRAYTONII*)

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Abstract.—We studied the microhabitat characteristics of 747 egg masses of the federally-threatened *Rana draytonii* (California Red-legged Frog) at eight sites in California. Our study showed that a broad range of aquatic habitats are utilized by ovipositing *R. draytonii*, including sites with perennial and ephemeral water sources, natural and constructed wetlands, lentic and lotic hydrology, and sites surrounded by protected lands and nested within modified urban areas. We recorded 45 different egg mass attachment types, although the use of only a few types was common at each site. These attachment types ranged from branches and roots of riparian trees, emergent and submergent wetland vegetation, flooded upland grassland/ruderal vegetation, and debris. Eggs were deposited in relatively shallow water (mean 39.7 cm) when compared to maximum site depths. We found that most frogs in artificial pond, natural creek, and artificial channel habitats deposited egg masses within one meter of the shore, while egg masses in a seasonal marsh averaged 27.3 m from the shore due to extensive emergent vegetation. *Rana draytonii* appeared to delay breeding in lotic habitats and in more inland sites compared to lentic habitats and coastal sites. Eggs occurred as early as mid-December at a coastal artificial pond and as late as mid-April in an inland natural creek. We speculate that this delay in breeding may represent a method of avoiding high-flow events and/or freezing temperatures. Understanding the factors related to the reproductive needs of this species can contribute to creating, managing, or preserving appropriate habitat, and promoting species recovery.

Key Words.—California Red-legged Frog; egg mass; habitat; lentic; lotic; oviposition; *Rana draytonii*; surveys

INTRODUCTION

The ability of populations to satisfy specific habitat requirements can affect the ability of a species to maintain stable or increasing population sizes. Rudolf and Rodel (2005) suggested that reproductive success of many organisms living in spatially and temporally variable environments may be strongly dependent upon the selection of appropriate oviposition locations during breeding. Marsh and Borrell (2001) suggested that oviposition strategies may be very flexible, which would allow species to adjust to different ecological contexts. Several studies suggest that female anurans select oviposition sites based on abiotic and biotic factors such as water depth at egg mass (Seale 1982), water temperature (Howard 1978), presence of conspecifics and congeners (Dillon and Fiaño 2000; Halloy and Fiaño 2000), or absence of predators (Howard 1978; Resetarits and Wilbur 1989). However, Rudolf and Rodel (2005) reported on the importance of including multiple biotic and abiotic factors in the analysis of oviposition site selection.

Further, they contend that the parameter combinations previously reported were often limited, and that manipulative experiments gave misleading predictions. Previous experimental works looked at a single habitat feature (e.g., presence of competitor or predator) while other factors remained equal. Rudolf and Rodel (2005) suggested that many authors neglected important inter- and intraspecific interactions or avoided considering combinations of parameters, which are typically found within natural systems. These restrictive assessments (i.e., manipulative experiments) of habitat conditions at oviposition sites could mischaracterize the importance of complex interacting parameters under natural conditions.

Rana draytonii has been studied extensively, but information on the characteristics of oviposition sites is extremely limited (USFWS 2002). Most reports of breeding habitat for this species are natural history accounts (Storer 1925; Stebbins 1954; Jennings and Hayes 1994; Lannoo 2005; Stebbins and McGinnis 2012). However, Cook and Jennings (2007) compared microhabitat characteristics of egg mass site

selection between *R. draytonii* and the American Bullfrog (*Lithobates catesbeianus*) at an emergent wetland. Typically, *R. draytonii* is reported to breed on the margins of slow moving lotic (e.g., freshwater ephemeral creeks) and lentic wetlands with open water (e.g., ponds), and deposit eggs at or near the water surface (Storer 1925; Stebbins 2003). Because of habitat alteration, most populations of this species currently rely on atypical and degraded breeding habitats (unpubl. data).

Although standards for amphibian survey methods have been developed (Heyer et al. 1994, Fellers and Freil 1995), surveys for individual species may require site or species specific modifications to standard techniques (e.g., timing, climatic associations, and microhabitat targeting) to increase reliability (Scherer 2008). *Rana draytonii* was listed as threatened pursuant to the federal Endangered Species Act in 1996 (USFWS 1996). The historic range of this frog has declined 70% due in large part to habitat loss from urban and agricultural development (Fisher and Shaffer 1996; USFWS 2002). Focused surveys are often required to evaluate development actions that may affect the status of this frog. Current field survey protocols include visual encounter survey techniques specifically for egg mass, larva, juvenile, and adult life stages (USFWS 2005). Although Fellers and Kleeman (2006) evaluated the effectiveness of survey protocols for juvenile and adult frogs, they did not study egg masses or larval stages. Recovery of this federally threatened species is dependent upon a better understanding of all of its life history requirements (USFWS 2002).

The goal of our study was to examine microhabitat characteristics of *R. draytonii* oviposition sites on a broad geographic range and in varied habitats. Specifically, we assessed the patterns of *R. draytonii* oviposition sites among habitat types that vary by geographic location, anthropogenic origin, and hydrologic and vegetative characteristics. We also discuss potential species-specific recommendations to aid in the effectiveness of field survey techniques for detecting egg masses. We believe that these actions will facilitate better understanding of the life history of this species, and aid in the recovery of this federally threatened species.

MATERIALS AND METHODS

Study sites.—Our eight study sites were

selected to encompass the regional distribution of *R. draytonii* and broad variation in habitat. The sites were located in the mountainous region of southern California, the coastal and inland San Francisco Bay Area, and the arid foothills of the western Great Central Valley (Fig. 1). Study sites differed in hydrology (e.g., lentic vs. lotic and hydroperiod), wetland vegetation composition, level of habitat disturbance or modification, and land management practices. We grouped study sites into four habitat types: Artificial Channel, Natural Creek, Artificial Pond, and Seasonal Marsh (Fig. 2; Table 1). Each of the authors collected data independent of one another over a 12-year period, with some field surveys overlapping years and some sites surveyed for multiple years (e.g., 2, 3, or 4 years at a single site; Table 2). Our data were assembled and analyzed *a posteriori*.

Field surveys.—Data for all sites were collected independently by the individual authors, in most cases during different years. Some data were mined from larger data sets that were collected for projects unrelated to this

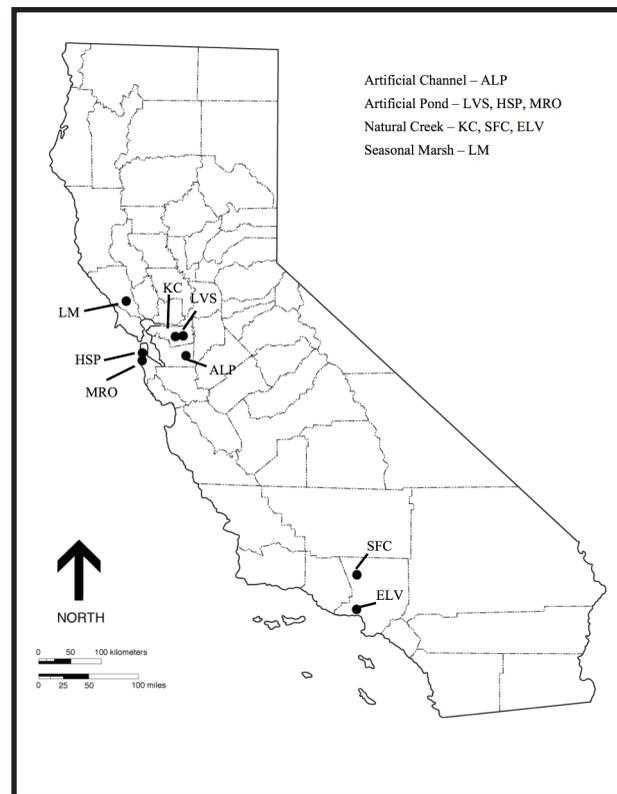


FIGURE 1. Location of eight *Rana draytonii* study sites within Alameda, Contra Costa, Los Angeles, San Mateo, and Sonoma Counties, California. Site codes are defined in Table 1.

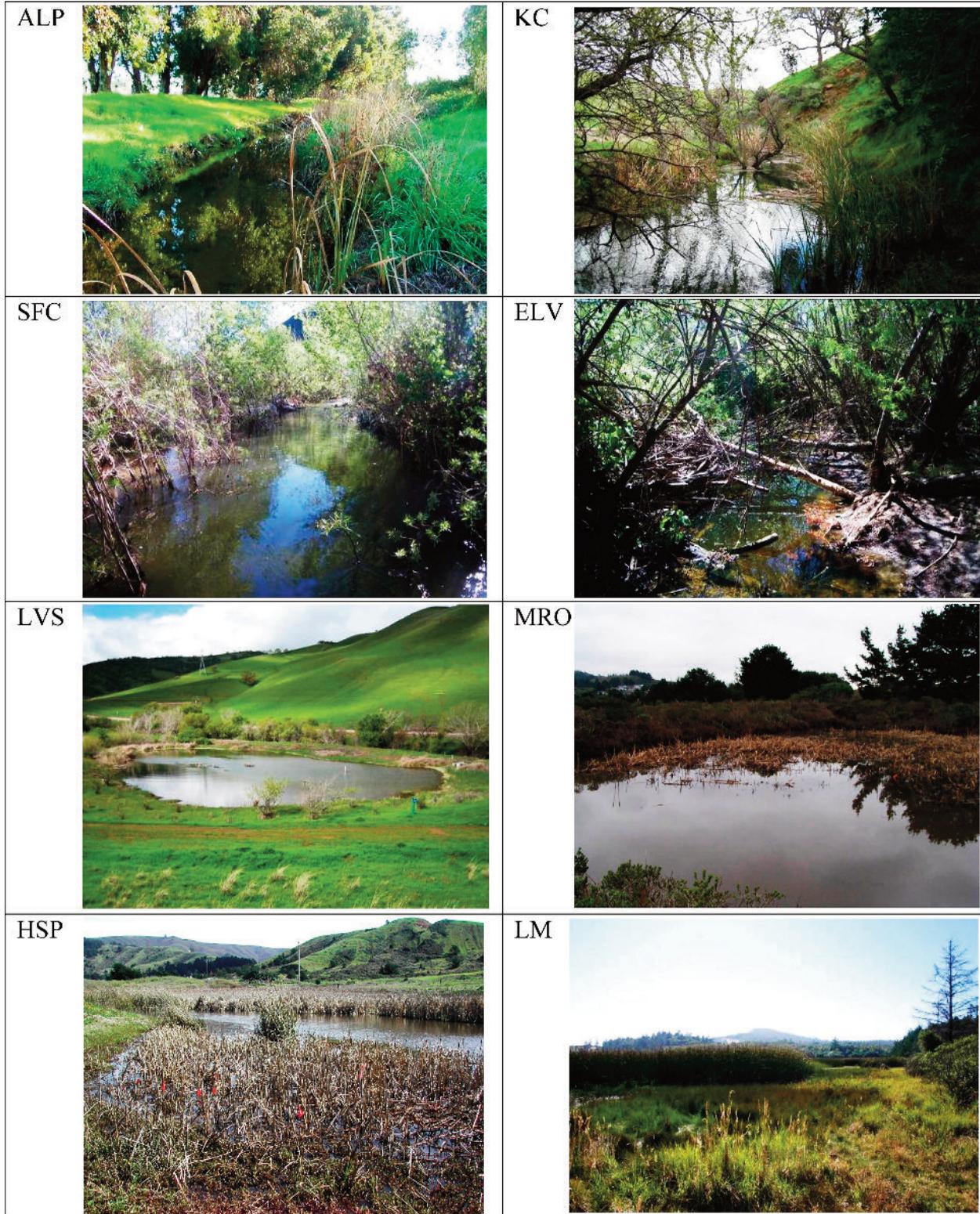


FIGURE 2. Photographs of *Rana draytonii* study sites. ALP = Arroyo Las Positas (photographed by Michael van Hattem); KC = Kellogg Creek (photograph by Jeff Alvarez); SFC = San Francisquito Creek (photographed by USGS); ELV = East Las Virgenes Canyon Creek (photographed by USGS); LVS = Los Vaqueros stock ponds (photographed by Jeff Alvarez); MRO = Milagra Ridge Oxidation Pond (photographed by Darren Fong); HSP = Horse Stable Pond (photographed by Darren Fong); LM = Ledson Marsh (photographed by David Cook).

TABLE 1. Habitat characteristics of eight *Rana draytonii* study sites. Sites are separated into lotic and lentic habitats and grouped into four habitat types.

Site Name	Hydrology (study site size/max. depth)	Site History and Habitat Characteristics	Surrounding Conditions
<u>LOTIC HABITAT: Artificial Channel</u>			
Arroyo Las Positas (ALP)	Perennial (2.5 km/150 cm)	Realigned engineered flood control channel constructed in 1944 and again between 1953 and 1981. Approximately 60% of ALP is perennial from treated groundwater discharge. Stream is a mosaic of open water and emergent hydrophytic vegetation. Banks consist of upland ruderal/grassland and emergent wetland vegetation dominated by Cattail (<i>Typha latifolia</i>) and to a lesser extent Narrow-leaf Willow (<i>Salix exigua</i>).	Surrounding land use includes industrial/campus, non-native annual grassland, and mixed commercial development including residential subdivisions.
<u>LOTIC HABITAT: Natural Creek</u>			
Kellogg Creek (KC)	Perennial (3.2 km/200 cm)	Natural creek below Los Vaqueros Reservoir. Mature riparian, including willows (<i>Salix</i> spp.), Fremont Cottonwood (<i>Populus fremontii</i>), and Valley Oak (<i>Quercus lobata</i>). The stream course consists of open water, bank wetland vegetation (e.g., cattail [<i>Typha</i> sp.] and Bulrush [<i>Schoenoplectus acutus</i>]), and debris dams and pools constructed by Beaver (<i>Castor canadensis</i>).	8,000-ha protected watershed. Managed for passive recreation, livestock grazing, and wildlife habitat.
San Francisquito Creek (SFC)	Perennial (2.5 km/200 cm)	Headwater creek in wide canyon. Former St. Francis dam at study site failed in 1928. Site burned in 2002. Winter floods buried stream channel with fine sediment. Stream habitat and riparian vegetation currently recovering and dominated by willow (<i>Salix</i> sp.), cattail (<i>Typha</i> sp.), and Watercress (<i>Nasturtium officinale</i>). Native and non-native fish present.	Angeles National Forest, Sierra Pelona Mountains. Stream flows in a 200-m wide riparian willow woodland surrounded by coastal sage scrub.
East Las Virgenes Creek (ELV)	Perennial (0.3 km/200 cm)	Headwater creek with 300 m of perennial flows and pools with thick riparian vegetation surrounded by grasslands. Site burned in 2005. Riparian vegetation dominated by willow (<i>Salix</i> sp.) and California Blackberry (<i>Rubus ursinus</i>). No fish present.	Upper Las Virgenes Open Space Park and Santa Monica Mountains National Recreation Area. Surrounding lands are rolling foothills with oak woodland and grasslands.
<u>LENTIC HABITAT: Artificial Ponds</u>			
Los Vaqueros Stock Ponds (LVS)	Perennial/semi-perennial (0.1–1.0 ha/ 50–200 cm)	Cattle stock ponds created between 1950 and 1980. Shorelines dominated by cattail (<i>Typha</i> spp.), bulrush (<i>Scirpus</i> spp.), and Spikerush (<i>Eleocharis macrostachya</i>) with open water in the center of ponds.	8,000-ha protected watershed. Managed for passive recreation, livestock grazing, and wildlife habitat.
Milagra Ridge Oxidation Pond (MRO)	Intermittent (0.17 ha /150 cm)	Abandoned oxidation pond on a closed military facility now a park. The pond was built prior to 1969. Dominant vegetation includes submerged annual grasses, spikerush (<i>Eleocharis</i> spp.), rushes (<i>Juncus</i> spp.), cattail (<i>Typha</i> spp.), and bulrush (<i>Scirpus</i> spp.).	Grassland, coastal scrub at park surrounded by urban development.
Horse Stable Pond (HSP)	Perennial (0.27 ha /180 cm)	Impounded coastal slough. Water levels are regulated by a pumping system that discharges into the ocean. Dominant vegetation includes cattail (<i>Typha</i> spp.) and bulrush (<i>Scirpus</i> spp.).	Pacific Ocean, grassland/costal scrub, coastal brackish marsh, golf course, urban development.
<u>LENTIC HABITAT: Seasonal Marsh</u>			
Ledson Marsh (LM)	Seasonal (11 ha/150 cm)	Marsh created in 1930 by a small earthen dam on existing wetland (Cook 1997). Patchy distribution of open water and dense marsh vegetation, including cattail (<i>Typha</i> spp.), spikerush (<i>Eleocharis</i> spp.), California Bulrush (<i>Schoenoplectus californicus</i>), and Smartweed (<i>Polygonum hydro Piperoides</i>).	2,000-ha State park. Managed for passive recreation and wildlife habitat.

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TABLE 2. *Rana draytonii* egg mass observations at eight study sites. Egg period is an estimate of the beginning of egg-laying through egg hatching. The LVS Pond egg period was relatively long due to local breeding variation among the 14 study ponds.

Habitat Type	Site	Year	Estimated Egg Period	Egg Masses	Habitat Total
<u>LOTIC HABITATS</u>					
Artificial Channel	ALP	2001	22 Feb–26 Mar	37	
	ALP	2002	4 Mar–13 Apr	32	
	ALP	2003	28 Feb–27 Mar	31	
	ALP	2004	5 Mar–2 Apr	9	109
Natural Creek	KC	2007	15 Feb–Mar 25	54	
	SFC	2003	6 Feb–20 Mar	13	
	SFC	2004	5 Feb–15 Mar	41	
	SFC	2006	10 Feb–22 Feb	8	
	ELV	2009	10 Feb–22 Mar	5	
	ELV	2010	25 Feb–24 Mar	28	149
<u>LENTIC HABITATS</u>					
Artificial Pond	LVS	2007	10 Jan–17 April	126	
	MRO	2005	11 Dec 2004–8 Mar	36	
	MRO	2006	19 Dec 2005–1 Mar	30	
	MRO	2007	1 Jan–24 Mar	31	
	HSP	2006	29 Dec 2005–17 Feb	43	
	HSP	2007	13 Feb–26 Mar	24	290
Seasonal Marsh	LM	1996	1 Feb–25 Feb	20	
	LM	1997	16 Jan–15 Feb	62	
	LM	1998	25 Jan–10 Mar	117	199
Total		747			

investigation. Our data collection techniques were similar as collecting data on egg masses is relatively standardized. We conducted diurnal visual encounter surveys at our eight study sites during the winter breeding period for *R. draytonii*. The start of surveys was adjusted to local breeding periods and annual weather conditions. Typically, sites were sampled at weekly intervals. We surveyed for egg masses by slowly walking along the shore of study sites and/or wading through wetland habitat to detect egg masses obscured by vegetation. Egg masses were positively identified (based on their size and shape, and absence of similar looking egg masses from other co-occurring species) mapped, and marked with flagging to avoid duplicate counting during subsequent visits.

We determined the period that eggs were laid and were potentially observable at each study

site annually by interpolating the onset of egg laying based on the timing of egg hatching. We determined this period of egg presence on embryonic stages observed during field surveys and an estimated embryonic growth rate of approximately one Gosner (1960) stage per day (DGC, unpublished data).

Microhabitat characteristics were measured at egg masses and included water depth at egg mass, depth from water surface to top of egg mass, egg mass attachment type (i.e., anchorage), and distance from the egg mass to the edge of the nearest shore. Water depths and distances associated with egg masses were measured using graduated measuring sticks or tapes. Maximum pool depth was estimated using dip nets placed into the presumed deepest portion of the pool.

Statistics.—We tested for differences in water depth at egg mass, egg mass depth, and distances from egg mass to shoreline from repeated surveys among habitat types by using mixed effects analysis of variance models (Littell et al. 1996; Zuur et al. 2009). We met the distributional assumptions of our models by normalizing egg mass attributes using Box-Cox transformations, where c rescales x to strictly positive values and λ is selected by maximum likelihood to optimize the transformation, while adjusting for potential year, site, or habitat differences (SAS Institute 2007). We evaluated spatial and temporal independence by comparing egg mass habitat characteristics models with and without random site or year effects, representative of covariance among different egg masses from within locations and years. We balanced the importance of these effects versus model parsimony by using restricted maximum likelihood to calculate Akaike's Information Criteria with 2nd order correction (AICc) based on a sample of 747 egg masses (Littell et al. 1996; Burnham and Anderson 2002) to compare the relative evidence in the egg mass data among four covariance models (site and/or year effects), including an independence model (no random effects). We selected models with the majority weight of evidence. Subsequently, we evaluated the fixed effects of habitat on water depth at the egg mass based on a model with random year effects, due to evidence of temporal dependence; depth of egg masses from the surface using a model with random site and year effects, because of evidence of both spatial and temporal dependence; and distance from egg mass to shore with an independence model (AICc weights = 0.73, 0.59, and 0.54, respectively).

We tested the effect of habitat at the $\alpha = 0.05$ significance level using the Satterthwaite calculation for degrees of freedom (Littell et al. 1996). If habitat was found to be a significant factor, we tested specific differences between habitat categories while applying the Tukey-Kramer adjustment for multiple comparisons. We computed means, based on back-transformed least squares estimates, and corresponding standard errors, based on the delta method, for each habitat type (Williams et al. 2002). For all analyses, we used SAS software (SAS Institute 2007), and Statistica software (StatSoft, Tulsa, Oklahoma, USA) to prepare box plots.

RESULTS

Our data included 747 *R. draytonii* egg masses during 12 study years between 1996 and 2010 (Table 2). The onset of egg deposition among sites and years ranged from 11 December to 5 March. Egg masses with developing embryos were present as late as 17 April. Most egg-laying occurred in about a 2–3 wk period at each study site, and embryos typically hatched within 2–3 wk at developmental stage 20 (Gosner 1960). Hence, the period when egg masses were present, and detectable at a study site typically ranged from 4–6 wk.

At our eight study sites we recorded 45 different egg mass attachment types. These attachment types ranged from branches and roots of riparian trees, emergent and submergent wetland vegetation, flooded upland grassland/ruderal vegetation, and debris (including submerged branches, fence posts, and bottom sediment). Both living and dead vegetation was utilized. The dominant egg attachment types by study site are listed in Table 3. At Ledson Marsh egg masses were commonly found unattached or loosely attached to dead stalks of Spikerush (*Eleocharis macrostachya*). Although at most study sites only a few attachment types were commonly used, we recorded up to 14 different types of anchorage at Arroyo Las Positas (Artificial Channel).

Rana draytonii deposited eggs in relatively shallow water (mean = 38 cm) among all study sites and habitat types (Fig. 3) compared to a site's maximum available depth (range = 50–200 cm; Table 1). When our model adjusted for unbalanced sample sizes and year variations, water depths at egg masses (mean \pm SE) were greatest at Artificial Ponds (51.1 \pm 6.2 cm) and Natural Creeks (42.5 \pm 5.1 cm), followed by Seasonal Marsh (37.7 \pm 7.2 cm) and Artificial Channel (23.0 \pm 3.5 cm). Although egg masses were mostly found in shallow depths (median = 31 cm), water depths at egg masses differed among our four studied habitat types ($F_{3,22.9} = 11.77, P < 0.0001$). Multiple comparisons using the Tukey-Kramer adjustments indicated that water depth was shallower for Artificial Channel egg masses than Artificial Ponds and Natural Creeks (Tukey-Kramer tests: $P < 0.0002$). Although the Artificial Channel estimate was also lower than Seasonal Marsh, there were fewer sites and years contributing to weak statistical difference (Tukey-Kramer: $P = 0.22$).

TABLE 3. *Rana draytonii* egg mass attachment types at eight study sites. Study years for a given site were grouped. Percentages in parentheses are use of an attachment type. Attachment types were defined coarsely and clumped subjectively: trees of different genera treated as a different attachment type; all annual upland grasses treated as a similar attachment type; herbaceous vegetation separated by genus.

Site Name	Primary and Secondary Egg Attachment Types	Number of Attachment Types
<u>LOTIC HABITATS</u>		
Arroyo Las Positas (ALP)	Annual upland grass (20%) Blue Gum (<i>Eucalyptus globules</i>) downed branches (16%)	14
Kellogg Creek (KC)	Debris (54%) Water Primrose (<i>Ludwigia</i> spp.; 26%)	6
San Francisquito Canyon Creek (SFC)	Horsetail (<i>Equisetium</i> sp.; 37%) Willow (<i>Salix</i> spp.; 24%)	7
East Las Virgenes Canyon Creek (ELV)	California Blackberry (<i>Rubus ursinus</i> ; 62%) Willow (<i>Salix</i> spp.; 31%)	3
<u>LENTIC HABITATS</u>		
Los Vaqueros Stock Ponds (LVS)	Cattail (<i>Typha</i> spp.; 63%) Green Algae (Chlorophyta; 10%)	9
Milagra Ridge Oxidation Pond (MRO)	Cattail (34%) Rush (<i>Juncus</i> spp.; 19%)	7
Horse Stable Pond (HSP)	Cattail (<i>Typha</i> spp.; 84%) Sedge (<i>Scirpus</i> spp.; 7%)	4
Ledson Marsh (LM)	Spikerush (<i>Eleocharis macrostachya</i> ; 57%) Narrow-leaf Cattail (<i>Typha angustifolia</i> ; 27%)	5

The occurrence of egg mass observations at or even above the water surface (46.2%) was relatively similar to submerged masses (53.8 %) among all habitat types. For all submerged egg masses, the mean depth (\pm SD) of the top of the egg mass below the surface was 9.5 cm \pm 8.8 cm. The deepest egg mass was 65 cm below the water surface at the Seasonal Marsh. When tested, there were no differences in water surface to top of egg mass depth among the four habitat types ($F_{3,5.1} = 0.22$, $P = 0.88$). There were 20 egg masses stranded above the water surface as much as 17 cm. Strandings occurred at Milagra Ridge Oxidation Pond, Ledson Marsh, and three egg masses were stranded but not measured at Horse Stable Pond. We speculated that these strandings were possibly the result of water level changes, movement of the vegetation, or other factors, none of which were directly witnessed by the authors.

Although there were significant differences in the distances of egg masses to the edge of the shore for all studied habitat types ($F_{3,395} =$

431.86, $P < 0.0001$), these distances were < 1 m for all habitats, except Seasonal Marsh (Fig. 4). The model-based shore distance at the Seasonal Marsh had a mean of 21.5 m and a maximum distance of 73.9 m. Multiple comparisons using the Tukey-Kramer adjustment indicated that Seasonal Marsh had the greatest distances, followed by Artificial Pond, Natural Creek, and Artificial Channels (Tukey-Kramer tests: $P < 0.02$ for all comparisons, except $P = 0.48$ for non-significant difference between Artificial Channel and Natural Creeks).

DISCUSSION

Habitat use.—Our observations indicate that a broad range of aquatic habitats are utilized by ovipositing *R. draytonii*, including sites with perennial and ephemeral water sources, natural and constructed habitats, lentic and lotic hydrology, and sites nested within modified urban areas or surrounded by protected lands. Although there was variation in microhabitat

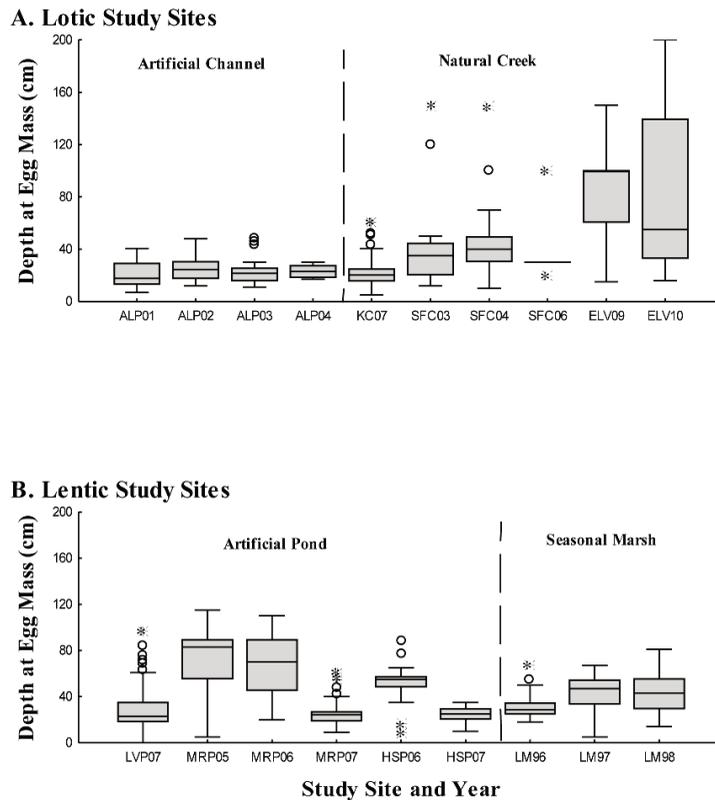


FIGURE 3. Water depths at *Rana draytonii* egg masses. The x-axis shows study sites by year. Dashed lines indicate sites grouped by habitat type. Boxes represent 25–75 percentile and median; circles represent outliers; asterisks are extreme outliers; and vertical bars are non-outlier ranges.

use, we typically found egg masses in shallow water, at or near the surface, in all of our studied habitats when a wide range of water depths is available. We did not, however, statistically analyze selection for shallow depths due to limited measurements at available and unused sites. We observed *R. draytonii* using 45 attachment types among study sites with the most common attachment types being live emergent vegetation. Storer (1925) reported that attachment to some type of substrate was necessary for *R. draytonii* so that egg masses would not sink. Although our observations were similar, we also found masses commonly at Ledson Marsh that were unattached or loosely attached to surrounding dead Spikerush stocks. Attachment to vegetation may be related to flotation or association with surface water temperatures, but may also function to moderate predation since vegetative cover would presumably be immediately adjacent to egg

masses for newly hatching larvae.

The location of deposited egg masses at the Artificial Channel, Natural Creek, and Artificial Pond habitats were near the shoreline (i.e., < 1 m). In contrast, egg masses at the Seasonal Marsh deviated from this spatial pattern by over 20-fold. The reason for this difference appears to be that the Seasonal Marsh contained broad shallow areas with extensive vegetative structure. At the other three studied habitat types steep banks and/or scouring flows during winter restricted vegetative structure to a narrow zone near the shore.

Biotic and abiotic factors.—We speculated that several factors may be working in concert in *R. draytonii*'s utilization of ovipositing microhabitats in our study. Abiotic factors, including water depth at egg mass, and perhaps solar orientation (i.e., utilization of the margins of vegetative cover) may have affected

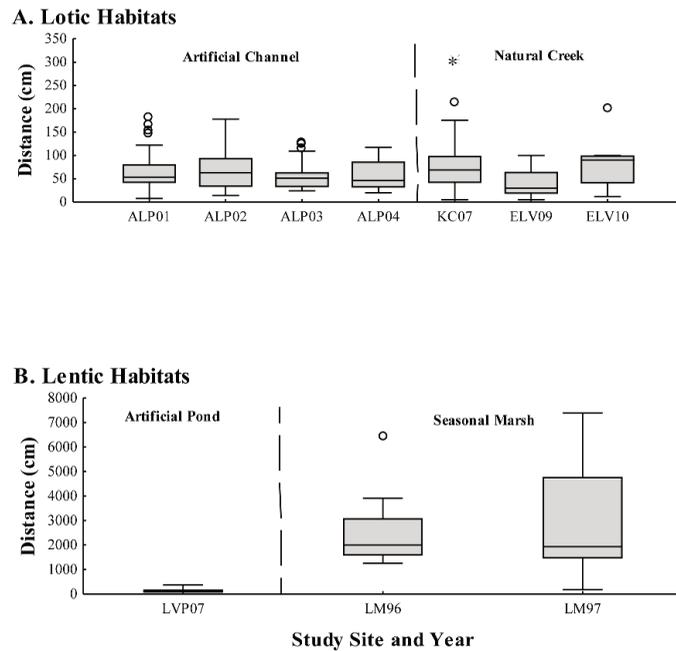


FIGURE 4. Distances from shore to *Rana draytonii* egg masses. Distance data were not collected for all study sites and years. The x-axis shows study sites by year. Y-axis scales are not equal. Dashed lines separate sites grouped by habitat type. Boxes represent 25–75 percentile and median; circles represent outliers; asterisks are extreme outliers; and vertical bars are non-outlier ranges.

placement of egg masses (Howard 1978; Seale 1982; Stebbins and Cohen 1995). The level of influence of these abiotic factors warrants further study. The dominant biotic factors in our study likely included vegetation availability and distribution as an anchorage for oviposition, and possibly the avoidance of predators (Resetarits and Wilbur 1989).

Due to the different search frequencies among sites, we did not attempt to statistically compare timing across major habitat types. Anecdotally, however, lentic and lotic conditions appeared to influence the timing of *R. draytonii* breeding, excluding the effects of seasonal weather conditions at our study sites. Although we observed considerable overlap in breeding periods (Table 1), our collective experiences at each study site indicated that *R. draytonii* breeds slightly later in lotic than lentic habitats. In the Seasonal Marsh ($n = 1$; surveyed 3 years) and Artificial Pond ($n = 16$; surveyed 1 year) habitats, breeding typically occurred from mid-January to mid-March, whereas at the Natural Creeks and Artificial Channel habitats—where high flows are frequent during winter—breeding

occurred mostly from mid-February through March. For example, during a single breeding season, observations within the lotic Kellogg Creek (Natural Creek) and lentic Los Vaqueros Stock Ponds (Artificial Ponds)—which occur in the same watershed—breeding was separated by over a month among these two habitat types. This pattern of delayed breeding has likely been exaggerated in the Artificial Channel where stream channelization and impervious surfaces within that watershed increase the number and intensity of pulsed flows. Seasonal delay of breeding in lotic habitats may reduce the risk of eggs being dislodged during high flows; as seen in the occasionally co-occurring *R. boylei* (Foothill Yellow-legged Frog; Wheeler et al. 2006). Although not specifically tested in our study, oviposition appeared to follow significant rain events, suggesting that climatic events that occur within the reproductive season influence timing and onset of major reproductive events.

Although not statistically tested, we inferred a geographic effect on the timing of *R. draytonii* breeding. Females within inland study sites typically began ovipositing later than coastal

sites. Horse Stable Pond and Milagra Ridge Oxidation Pond are located along the Pacific coast and had breeding as early as early December. In contrast to coastal sites, breeding began in mid- to late-January at inland lentic sites. Presumably, this pattern is consistent with moderate coastal conditions that reduce the threat of freezing temperatures through much of winter, to which this species is not typically exposed (Storer 1925).

Ovipositing nearer to the shore edge in lotic habitats may protect egg masses from washing down stream during high flow events. Wheeler et al. (2006) documented similar patterns of habitat utilization in the stream-breeding *R. boylei*. Proximity to shore can also be important to avoid aquatic predators (Licht 1969). Invasive predatory fishes are common in the Natural Creek (e.g., Green Sunfish [*Lepomis cyanellus*]). We suggest that eggs deposited near shore and within vegetative cover would allow newly hatched tadpoles to benefit from a reduced risk of predation due to the proximity to physical cover and shallow water at hatching (Resetarits and Wilbur 1989). However, predation risk is confounded by the breadth of microhabitat utilization of multiple non-native species. In the Natural Creek and Artificial Channel, *R. draytonii* co-occur with Mosquitofish (*Gambusia affinis*), which utilize slow flowing and shallow water habitats. The Mosquitofish is a non-native species known to reduce the overall fitness of *R. draytonii* (Lawler et al. 1999). Reduced fitness (i.e., reduced size at metamorphosis) does not necessarily equate to a reduction in recruitment, therefore, shallow water oviposition site selection may remain effective when multiple non-native predatory fish species are present.

Our statistical models confirmed similar patterns among habitat types that were demonstrated graphically, but are not free of potential biases (Figs. 3 and 4). We assumed that the collected egg masses were representative and unbiased samples of all egg masses at those habitat types and in those years when they were sampled. If this assumption is untrue, then the results of both the statistical and the graphical analyses are subject to biased habitat comparisons. We also used statistical models to compare habitat types while adjusting for uneven sampling across sites and years, which requires that those effects be independent; we assumed that site differences were similar within each

year. Our tests comparing habitat types are robust relative to temporal variations under the assumption that those variations are independent of site, but can be substantially biased if not.

Management recommendations.—The broad range of microhabitats utilized by *R. draytonii* for oviposition suggests that field investigators should adjust egg mass visual encounter techniques as local and specific habitat conditions dictate. Surveys should be completed within the anticipated 4–6 wk period when egg masses are detectable. If the local breeding period is unknown, visual surveys can be conducted ideally at 2–3 wk intervals with a maximum interval of 4–6 wk. Although most egg masses occur at or near the water surface, searches to depths of approximately 60 cm should only be conducted with water visibility adequate to see egg masses on the bottom in order to avoid stepping on masses. Surveyors should focus on detecting egg masses by searching in and around emergent and submergent vegetation and debris. Further, surveyors may increase success by focusing their observation area to within 1–2 m of the shore in lotic habitats and ponds. The exception to this guideline is marsh habitats or ponds that are functioning as marshes (i.e., shallow with extensive emergent vegetation). These habitats should be surveyed by slowly walking along transects, in the water, throughout the accessible aquatic habitat.

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