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Foothill Yellow-Legged Frog (*Rana boylii*) Oviposition Site Choice at Multiple Spatial Scales

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ABSTRACT.—**Studies of resource selection at multiple scales are critical to understanding ecological and evolutionary attributes of a species. We analyzed relative abundance, habitat use, and oviposition site selection of Foothill Yellow-Legged Frogs (*Rana boylii*) at 11 localities across two geographic regions in California (northern Coast Range and Sierra Nevada) over 16 yr. We found narrow ranges for oviposition microhabitat characteristics (water depth, water velocity, and stream substrate) among study localities. At the Main and South forks of the Trinity River, variances of the habitat traits were lower for oviposition microsites than for random points within breeding areas, indicating fine-scale selection. On the South Fork Trinity, egg mass relative abundances were negatively associated with water depth and positively associated with distance from the shoreline, suggesting that breeding areas with high egg mass relative abundances generally occurred in wide shallow areas. We observed long-term repeated use of breeding sites. At the South Fork Trinity, 63% of potentially suitable breeding areas were used consecutively for 3 yr, and at Hurdygurdy Creek several areas were used in ≥11 yr. Oviposition site selection and microhabitat specificity may result in population stability even within the substantial temporal and spatial variability of stream environments. Management of stream environments and conservation plans for *R. boylii* could benefit by preserving hydrologic processes that produce these specific habitats and identifying and protecting high-use breeding areas.**

The physical environment is the matrix within which organisms hone their ecological strategies and test their evolutionary mettle (Southwood, 1977, 1988). A detailed knowledge of a species' habitat relationships is essential for understanding that organism's fundamental strategies for persistence (Holt, 1987). Plasticity in a life-history trait like habitat choice can be particularly vital in stochastic or seasonally changing environments (Fretwell, 1972). Because amphibians have multiple life stages (i.e., complex life cycles; Wilbur, 1980), unraveling stage-specific habitat relationships and overall implications for species persistence can be particularly challenging (Biek et al., 2002). Information on habitat associations can contribute to an understanding of species' population dynamics and lead to more effective conservation and management approaches (Morris, 2003). The ability to quantify characteristics of environments that promote high fecundity and survival rates provides an important first step in improving management and restoring altered habitats for imperiled species. The surrounding environment (e.g., vegetation structure, hydrology, temperature) often is one of the only aspects of a species' ecology that can be immediately managed. Biologists and managers frequently use information on habitat associations for at-risk species in land and water management planning and decision making. Studies often focus on small-scale (microhabitat) habitat use, however, and the information gathered may not be useful to managers who need to address large-scale human-caused disturbances (Fausch et al., 2002).

Rana boylii historically occurred in foothill and mountain streams (to 1,830 m) from northern Baja California, Mexico to southern Oregon west of the Sierra–Cascade crest, and has experienced significant population declines (Jennings and Hayes, 1994; Jennings, 1996; California Department of Fish and Game, 2005). It is one of a few western North American anurans that is exclusively associated with running waters (lotic environments). Breeding and oviposition occur from spring to early summer along streams in relatively open areas where females attach a single egg mass to pebbles or cobbles on or near the bottom of shallow, low water velocity areas (Fellers, 2005). Tadpoles develop in and near oviposition areas and metamorphose in early autumn (Nussbaum et al., 1983). Prior research confirms historical observations of habitat associations (Kupferberg, 1996; Lind et al., 1996), and Bondi et al. (2013) recently developed and tested habitat suitability models for oviposition and tadpole sites in the Sierra Nevada region. Here, we examined habitat associations of *R. boylii* at multiple scales for an extensive portion of the species' geographic range in California. We also studied long-term site fidelity to areas used for reproduction by *R. boylii*, a species capable of living up to 13 yr (Hayes et al., in press).

Habitat requirements and factors that limit animal distribution and abundance patterns vary at different scales, and species occurrence may be better predicted by variables at one scale relative to another (Fausch et al., 2002; Boyd et al., 2008; Saavedra-Rodríguez et al., 2012). For *R. boylii*, a lotic species that has adapted to conditions in a seasonally dynamic environment at multiple scales, understanding these associations and long-term patterns in habitat use may be useful in the development of effective management options and conservation strategies. This is particularly important for populations in regulated (dammed or diverted) streams where alterations in stream habitat characteristics, such as channel morphology, and flow and temperature regimes, may be apparent at multiple scales. Our objectives were to 1) quantify multiscale oviposition microhabitat associations of *R. boylii* in California's northern Coast Range and Sierra Nevada regions, from the broad stream reach (segment) to the local scale of breeding area, down to the fine-scale microenvironment oviposition sites, 2) compare our findings with habitat suitability criteria established for Sierra Nevada populations, 3) examine egg mass relative abundance over multiple breeding seasons and relate it to breeding area characteristics, and 4) document breeding area site fidelity. The long-term data collection at some localities combined with data from robust populations in several geographic locations provide key information for land managers and baseline data for future monitoring and research on this declining amphibian.

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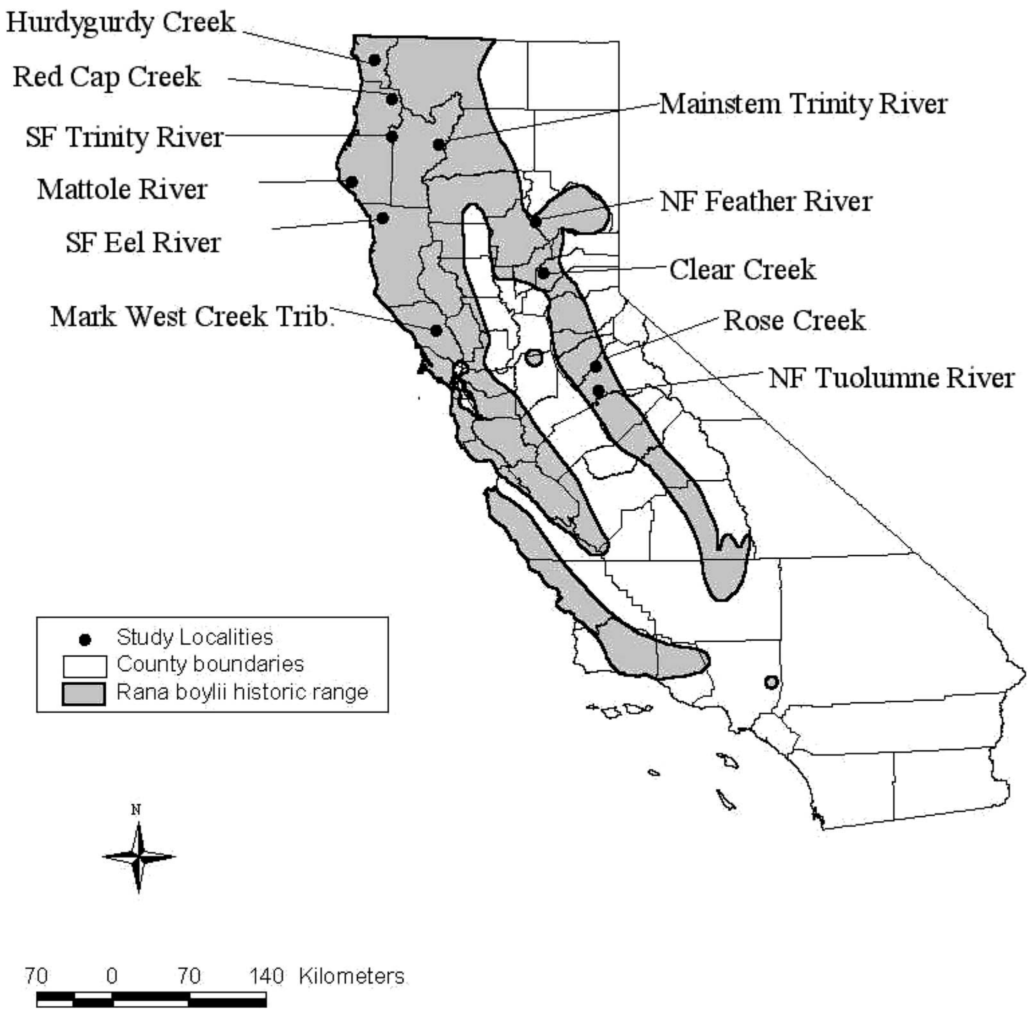

FIG. 1. *Rana boylii* study localities and historic distribution in California.

MATERIALS AND METHODS

Study Sites.—We collected *R. boylii* habitat association data at 11 localities—7 in the northern Coast Range region and 4 in the central and northern Sierra Nevada of California (Fig. 1). The northern Coast Range region included areas north of San Francisco Bay and west of the Sacramento River drainage in California; the Sierra Nevada region was synonymous with the mountain range of the same name in eastern California. We evaluated oviposition microhabitat use at all 11 localities. We examined microhabitat selection, relative abundance of egg masses, and breeding area characteristics and use in detail at 3 of the 7 localities in the northern Coast Range of California (Hurdygurdy Creek, Main Fork Trinity River, and South Fork Trinity River) (Fig. 1). We use "stream" throughout this paper to designate both creeks and rivers.

Microhabitat Use and Selection.—We gathered data on oviposition microhabitat of *R. boylii* over 12 yr (1991–2002). These data were collected by several individuals for various research projects and the dates and the frequency of surveys were based on the specific breeding periods for each sampling locality; however, the methods of data collection were standardized. For all localities, we recorded water velocity, water depth, water temperature, and distance from shore. For north Coast Range localities, we also collected stream mesohabitat type (e.g., pool, riffle, run), substrate size, attachment substrate, orientation of egg mass, and direction of water flow. Variables were measured immediately adjacent to each egg mass (= microhabitat variables; detailed methods in Lind, 2005). Water temperature was not used in any analyses because of the unreliability of the method of data collection; measurements were recorded at different times of the day and in habitats that tend to be highly variable (i.e., the shallow water within stream bars). We compared differences among streams and regions using descriptive statistics without specific hypothesis testing.

We collected data on microhabitat characteristics of egg mass positions and randomly selected points within each breeding area at two localities—the Main Fork and South Fork of the Trinity River in the spring of 1992. On the basis of literature accounts and experience, we defined potential breeding habitat as the stream environments along sparsely vegetated rocky stream bars (geomorphologic features created by deposition of stream-mobilized sediments [all sizes] in areas of reduced water velocity, such as the inside of stream bends [Trush et al., 2000]). We assessed availability of habitat attributes by collecting data from points along line transects placed near egg masses. Transects were systematically spaced on the basis of the long axis of the shore, with a minimum of two at any given stream bar. They were placed perpendicular to the shoreline and extended out into the river 1 m beyond the farthest egg mass in the same area. We recorded data at either 0.5-m, 1-m, or 2-m point intervals, depending on the total length of each transect so that we recorded at least three points (and typically no more than six) per transect. At each point we recorded: distance from shore (m), water depth (cm), and water velocity (m/s). For analysis, we randomly selected one of the "available" points from each line transect adjacent to each egg mass microsite and treated the point location with the egg mass (used) and the randomly selected point (available) as paired data. We expected used sites to exhibit less variability than the surrounding available environment, but to necessarily be a subset of that environment. We computed means and variances for used and available point data from all breeding areas at each locality and used a multivariate paired *t*-test (Hotelling's *t*-square) to evaluate use vs. availability for three variables: water depth, distance from shore, and water velocity. This analysis was followed by univariate paired *t*-tests of each variable to provide better resolution of the overall difference. We compared the variances of paired samples using a modified *t* statistic (Snedecor and Cochran 1989: 196–197) for each of the three variables. We used a Bonferroni-adjusted significance level of $\alpha = 0.017$. Because we collected data on a single occasion, we likely did not detect all egg masses deposited during the breeding season, so some random sites may have been used as oviposition sites after our sampling occurred. Microenvironmental conditions at random sites also would have presumably changed as the breeding season progressed.

Relative Abundance and Breeding Area Use.—We studied relative abundance of egg masses and breeding area use across multiple years at three stream localities: Hurdygurdy Creek, Main Fork Trinity River, and South Fork Trinity River. We documented reproductive activities at Hurdygurdy Creek with surveys during breeding seasons from 1987 to 2002, but we did not record detailed data in all years. We typically conducted one survey for egg masses or tadpoles in the spring and another survey for tadpoles in midsummer of each year. During surveys at this locality, two to three observers (at least one on each stream bank) waded upstream searching the nearshore environment of a 4.7-km stream reach. We counted egg masses and located them on a map of stream mesohabitat units (e.g., riffle, run, pool) that was developed to study an ophidian frog predator (*Thamnophis atratus hydrophilus*) at the same locality (Welsh et. al, 2010).

We conducted multiyear surveys of breeding areas at the Main Fork Trinity River from 1991 to 1994 and at the South Fork Trinity River from 1992 to 1995. Results from the Main Fork Trinity surveys were presented elsewhere (Lind et al., 1996) and are included only in the Discussion of this paper. At the South Fork Trinity River locality, we conducted surveys on a 15.6-km section of the river over several days each spring. Observers traveled downriver by boat and stopped to survey all bars >5 m long. Each bar was uniquely numbered and mapped on an aerial photograph. One observer searched each bar and nearshore waters by walking along the shoreline, first upstream and then downstream. We conducted one survey of each river bar, counted individual egg masses, and later performed an additional survey of river bars to document tadpole presence. We searched all bars in the 15.6-km reach ($n = 80$) in 1992–1994, and revisited a subset ($n = 29$) on a 5.7-km section of river in the middle of the study reach in 1995. We analyzed data for both the 80 bars surveyed for 3 yr and the 29 bars surveyed in all 4 yr.

We summarized egg mass counts at Hurdygurdy Creek and South Fork Trinity River relative to the total length of each study area. At Hurdygurdy Creek, because of the observational and opportunistic nature of the data collection, we used a subset of 5 yr (1991, 1992, 1998, 1999, 2000, in which standardized surveys were done) to develop estimates of the relative abundance. Having habitat availability data for the South Fork Trinity from 1992 (described above) allowed us to examine factors that were predictive of egg mass relative abundance (egg masses/m). We collected habitat variables and conducted a single-visit egg mass survey for 30 randomly selected stream bars along the South Fork Trinity River in May of 1992. We used stream bar as the unit of analysis and all points along line transects (rather than one random point per transect) to derive means for three continuous variables: distance from shore, water depth, and water velocity. We calculated the number of egg masses per meter to account for variation in stream bar lengths. We used generalized linear models and applied Akaike information criterion (Akaike, 1973) corrected for small sample size (AIC_c; Burnham and Anderson, 2002) to determine the "best" combination of stream-bar variables that were associated with egg mass relative abundances. Egg mass relative abundances exhibited substantial departure from normality and were natural log transformed.

We examined repeated use of breeding areas (gravel bars for the South Fork Trinity River localities and mesohabitat units for Hurdygurdy Creek) over the years and calculated the percentage of bars used each year or range of years. We defined use as the presence of either egg masses or tadpoles during the breeding season or tadpoles later in the summer. For Hurdygurdy Creek, we identified oviposition "hot spots" as those stream mesohabitat units observed to contain egg masses or tadpoles in at least one-third of the total years of this study (6 or more of 16 yr). We mapped all breeding areas using ArcView 3.2 GIS (Environmental Systems Research Institute, Redlands, California, USA), but we calculated nearest-neighbor distances between breeding areas and distances from breeding areas to tributary streams just for hot spots. We computed these distances using the measuring tool available in the GIS software.

We conducted all statistical analyses using SAS v.8 (SAS Institute, Cary, North Carolina, USA).We examined the normality of all variables and, except for egg mass relative abundance, found only minor departures from normality; no other variables were transformed (Huber, 2011). Results of descriptive statistics are reported as means ± SD.

RESULTS

Microhabitat Use and Selection.—The four continuous variables describing oviposition microhabitats (water velocity, water depth, distance from shore, and surrounding substrate size) fell in fairly narrow ranges both within and across localities (Table 1). Most egg masses among all north Coast Range localities were attached to cobble and boulder substrates in glide and edgewater pool mesohabitats. Egg masses were typically attached on the downstream side of substrates in such a way that water flowed alongside the mass (Fig. 2).

For the Main Fork Trinity River, we found differences between used and available microhabitat both in the multivariate means and in the univariate variances of point characteristics. Mean water velocity was lower, and variances in water depth and water velocity were lower for used microhabitat (oviposition sites) compared with available microhabitat (random points) (Table 2). For the South Fork Trinity River, we found no difference in the means between used and available site microhabitat attributes, but the variance in water depth was lower for used sites compared with available sites, indicating

TABLE 1. Summary statistics for variables describing oviposition microhabitat of Foothill Yellow-Legged Frogs (*Rana boylii*) from 11 streams in California (see Fig. 1). [a] Streams regulated by upstream dams. Substrate size is a weighted mean.

Stream locality	Estimated drainage basin area (km^2)	Yr	Study reach (km)	Water velocity (m/s)		Water depth (cm)		Distance from shore (m)		Substrate size (mm)	
				n	Mean (SD)	*n*	Mean (SD)	*n*	Mean (SD)	*n*	Mean (SD)
North Coast Range											
Hurdygurdy Creek	77	1991–1994	4.70	28	0.034 (0.027)	28	13.54 (3.64)	28	1.50 (0.89)	28	112.8 (43.6)
Red Cap Creek	163	1994	0.10	5	0.010 (0.000)	5	9.10 (1.81)	5	0.44 (0.15)	5	58.5 (1.8)
Main Fork Trinity River[a]	5,278	1991–1994	22.50	77	0.044 (0.040)	77	21.34 (7.17)	77	2.68 (2.27)	78	80.9 (23.2)
South Fork Trinity River	2,414	1992–1995	15.60	52	0.036 (0.035)	52	21.33 (6.43)	52	2.13 (1.56)	52	82.7 (43.1)
Mattole River	768	1994–1995	0.10	23	0.049 (0.031)	26	12.20 (5.48)	26	3.79 (3.60)	26	113.4 (23.3)
South Fork Eel River	1,785	1994	0.10	16	0.044 (0.032)	16	14.99 (3.61)	16	1.81 (1.99)	16	147.3 (25.4)
Mark West Creek Tributary	0.4	1995	0.10	-	-	6	13.25 (5.38)	8	0.55 (0.51)	8	66.6 (58.6)
Sierra Nevada											
North Fork Feather River[a]	3,052	2002	1.00	4	0.038 (0.043)	4	32.25 (5.56)	4	1.68 (0.046)	-	-
Clear Creek	7	1993–1995	0.81	18	0.009 (0.009)	35	11.83 (3.85)	43	0.50 (0.33)	-	-
Rose Creek	110	2001	0.65	-	-	10	21.20 (7.93)	14	1.11 (0.35)	-	-
North Fork Tuolumne River	258	2001	0.30	-	-	3	21.33 (9.02)	3	0.70 (0.44)	-	-

that microenvironments used for oviposition represented a specific subset of conditions within the available environment (Table 2).

Relative Abundance and Breeding Area Use.—At South Fork Trinity River, egg mass relative abundances were high and consistent among years, with egg mass counts of 548–731 in 15.6 km (Fig. 3a). At Hurdygurdy Creek, egg mass relative abundances also were consistently high but lower than South Fork Trinity relative abundances. We recorded 84–140 egg masses in 4.7 km (Fig. 3b).

For South Fork Trinity River breeding areas, distance from shore (+) was the only mesohabitat variable in the top-ranked model explaining *R. boylii* egg mass relative abundance (Akaike weight $w_i = 0.43$, Table 3). The next best model included both

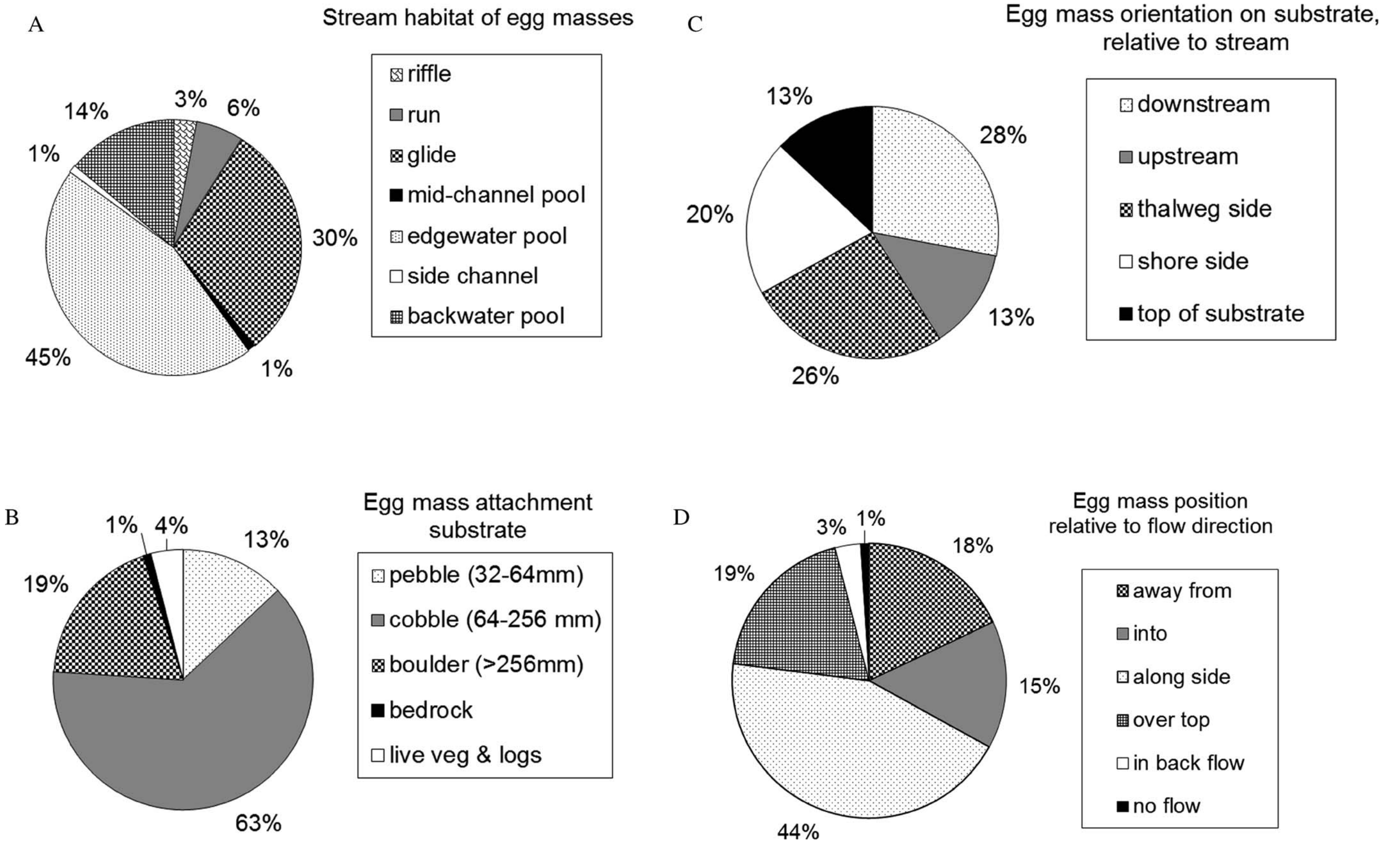

FIG. 2. Egg deposition site characteristics by (A) stream habitat type (Hawkins et al., 1993), (B) egg mass attachment substrate, (C) orientation of egg masses on substrate relative to stream, and (D) direction of water flow for *Rana boylii* at northern Coast Range localities from 1991 to 1995.

TABLE 2. Descriptive statistics and *t*-test results for Foothill Yellow-Legged Frog (*Rana boylii*) oviposition habitat selection at the Main Fork ($n = 31$) and South Fork ($n = 48$) Trinity rivers. Paired egg mass microhabitat points and available habitat points were analyzed relative to distance from shore, water depth, water velocity, and water temperature. Significant results ($\alpha = 0.017$ after Bonferroni adjustment) are in bold text.

		Main Fork				South Fork			
Microhabitat characteristic	Available (A) or used (U)	Mean	*t*-test of mean	Variance	*t*-test of variance	Mean	*t*-test of mean	Variance	*t*-test of variance
Distance from shore (m)	A	2.48	$t = 0.86$	6.19	$t = 2.04$	2.1	$t = 0.62$	2.06	$t = 0.81$
	U	2.01	$P = 0.394$	2.96	$P = 0.051$	2.19	$P = 0.543$	2.56	$P = 0.403$
Water depth (cm)	A	27	$t = 1.45$	**238.07**	**$t = 3.80$**	19.77	$t = 0.62$	**126.34**	**$t = 5.79$**
	U	23.87	$P = 0.157$	**54.31**	**$P < 0.001$**	20.55	$P = 0.540$	**36.66**	**$P < 0.001$**
Water velocity (m/s)	A	**0.095**	**$t = 2.89$**	**0.008**	**$t = 5.75$**	0.041	$t = 0.72$	0.002	$t = 2.20$
	U	**0.053**	**$P = 0.007$**	**0.002**	**$P < 0.001$**	0.036	$P = 0.475$	0.001	$P = 0.033$

distance from shore (+) and water depth (−) and had a similar Akaike weight as the top model (Table 3). The positive relationship with distance from shore combined with the negative relationship with water depth is indicative of wide shallow areas as providing optimal breeding habitat (Fig. 4).

At the South Fork Trinity River, 51 of the 80 river bars were used for breeding in all 3 yr and 21 of the subset of 29 bars were used for breeding in all 4 yr (Fig. 5a). Of the 51 mesohabitat units found to have breeding over 16 yr at Hurdygurdy Creek, 36 were used for oviposition in ≤5 yr and 15 (hot spots) were used in ≥6 yr (Fig. 5b). The annual average egg mass count for the 15 hot spots over the entire 16 yr was 7. One mesohabitat unit accounted for 39% of hot-spot production, with 26 ± 15.2 egg masses per year and evidence of reproduction (as either eggs or tadpoles) in all years. Results from the spatial analysis indicated that the average stream distance between all nearest-neighbor pairs of breeding hot spots was about 0.33 ± 0.29 km and the average distance to the closest tributary (upstream or downstream) was 0.79 ± 0.63 km. All hot spots were associated with "braided" (multichannel) areas of the stream; 73% were immediately upstream of these areas and 27% were in secondary channels within such areas.

DISCUSSION

Understanding a species' ecological requirements is often limited by the examination of habitat use at just one particular scale (e.g., microhabitat), and management recommendations based on such information may not be effective when dealing with large-scale disturbances (Fausch et al., 2002). Fausch et al. (2002) advised using a multiscale ("riverscape") approach to study habitat heterogeneity and habitat needs of fish in lotic environments, but this concern is relevant to the conservation of other stream organisms such as *R. boylii*, where the primary threats are large human-caused disturbances such as dams and diversions. Studies have documented *R. boylii* habitat selection at microenvironmental and stream reach spatial scales (Kupferberg, 1996; Bondi et al., 2013). We extended this previous work to a larger geographic area, strengthening the evidence for habitat selection of particular environments at multiple scales, and we documented long-term site fidelity to breeding areas. Our analyses indicate that for oviposition, *R. boylii* prefers shallow, low water velocity areas in locations protected from extreme flows dominated by cobble-sized substrates. We found that a narrow range of environmental conditions was used for *R. boylii* oviposition sites in small and large streams and from the northern Coast Range to the Sierra Nevada. Results from the Trinity River Basin provided evidence that these conditions were selected for; the oviposition site characteristics were less variable than the surrounding environment. Long-term monitoring of breeding activity along two streams indicated that frogs exhibited breeding site fidelity to areas along streams that consistently provided suitable oviposition habitat. The geographic scope of our work suggests that these affinities may be pervasive in *R. boylii* and reinforces the notion that this species is susceptible to modifications to breeding habitats and the associated characteristics necessary for successful reproduction.

Microhabitat Use and Habitat Selection.—The relatively narrow ranges of environmental conditions used by breeding *R. boylii* are consistent with earlier qualitative descriptions (Storer, 1925; Fitch, 1936; Zweifel, 1955) and quantitative work (Kupferberg, 1996; Bondi et al., 2013). *Rana boylii* oviposition sites at localities that were widely separated geographically and with substantial variability in stream size demonstrated surprisingly similar

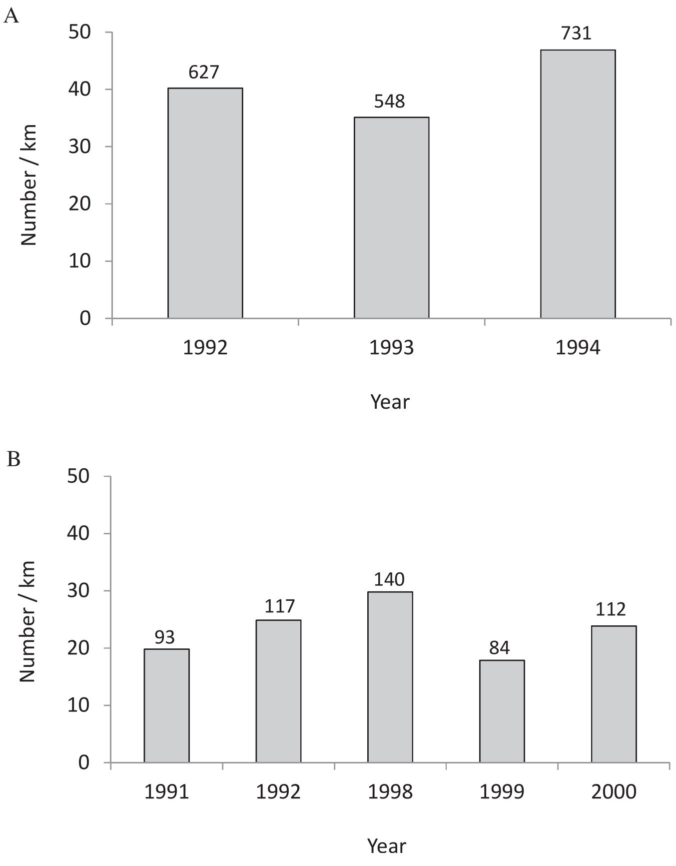

FIG. 3. Relative abundance of *Rana boylii* egg masses at (A) South Fork Trinity River (numbers above each bar are the total number of egg masses in the 15.6-km study reach), and (B) Hurdygurdy Creek (numbers above each bar are the total number of egg masses in the 4.7-km study reach).

TABLE 3. Candidate models for stream bar habitat associations with *Rana boylii* egg mass relative abundance. The direction of effect for each variable included in a model is indicated as positive$^{(+)}$ or negative$^{(-)}$.

Model	AIC$_c$	ΔAIC$_c$	Weighted Akaike w_i	Evidence ratio
Distance to shore$^{(+)}$	−125.31	0.00	0.43	1.00
Distance to shore$^{(+)}$ + water depth$^{(-)}$	−124.64	0.67	0.31	1.40
Distance to shore$^{(+)}$ + water velocity$^{(-)}$	−122.63	2.68	0.11	3.82
Distance to shore$^{(+)}$ + water velocity$^{(-)}$ + water depth$^{(-)}$	−121.91	3.40	0.08	5.47
Water depth$^{(-)}$	−120.73	4.58	0.04	9.87
Water velocity$^{(-)}$ + water depth$^{(-)}$	−118.61	6.70	0.02	28.50
Water velocity$^{(-)}$	−117.04	8.27	0.01	62.49

characteristics, though standard deviations were large at some localities (Table 1). These results highlight the need for collection of site-specific ambient environmental conditions to better understand habitat use and selection. Bondi et al. (2013) found that habitat suitability criteria developed using data from large rivers in the Sierra Nevada performed poorly in predicting suitability of breeding habitat along smaller Sierran streams.

In our study, water velocities at oviposition sites along north Coast Range streams (0.010–0.049 m s^{-1}) were similar to the mean velocity of Sierran oviposition sites (0.05 m s^{-1}) used in developing habitat suitability criteria (Bondi et al., 2013) and velocities for our north Coast Range sites fell within the range of values deemed suitable (0.00–0.15 m s^{-1}) by Bondi et al. (2013). Water depths for north Coast Range oviposition sites (0.091–0.213 m) generally were shallower compared with those at our Sierra Nevada sites (0.118–0.322 m) and Sierran streams from the habitat suitability study (0.39 m; Bondi et al., 2013), but mean water depths at oviposition sites along most north Coast Range streams were within or just below the range of suitable values (0.14–0.67 m) according to Bondi et al. (2013). Although similar to the Sierran study in that egg mass attachment substrates were predominantly boulder and cobbles (Bondi et al., 2013), we found that cobbles were the primary attachment substrate for egg masses (63%), followed by boulders (19%) at north Coast Range sites, whereas Bondi et al. (2013) found that boulders were the predominant substrate used for oviposition. We did not measure substrate availability but we suspect that this discrepancy is a consequence of differences in stream-bed substrate composition. Bondi et al. (2013) suggested that poor performance of their habitat suitability criteria on smaller Sierran streams may have been a result of shallower depths and finer substrates and therefore locally derived criteria may be needed.

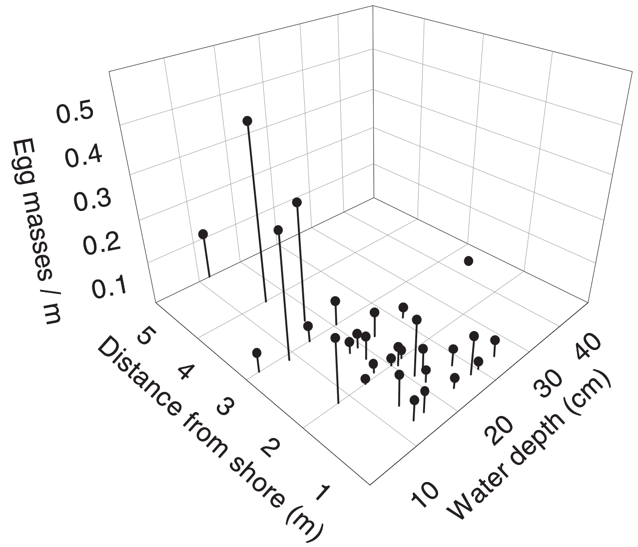

FIG. 4. Relationship between egg mass relative abundance and mean distance from shore and water depth ($n = 30$ stream bars) for the South Fork Trinity River in 1992. Egg mass relative abundances are presented as number/m.

Narrower variances in water depths and water velocities at oviposition (used) sites compared with random (available) sites along the Main and South forks of the Trinity River were further evidence of habitat selection. Results suggest that frogs selected shallower and lower flow habitats at both localities regardless of flow regime, though the mean water depth and water velocity and the variance of all parameters of used and available sites was higher for the Main Fork Trinity (regulated) compared with the South Fork Trinity (unregulated).

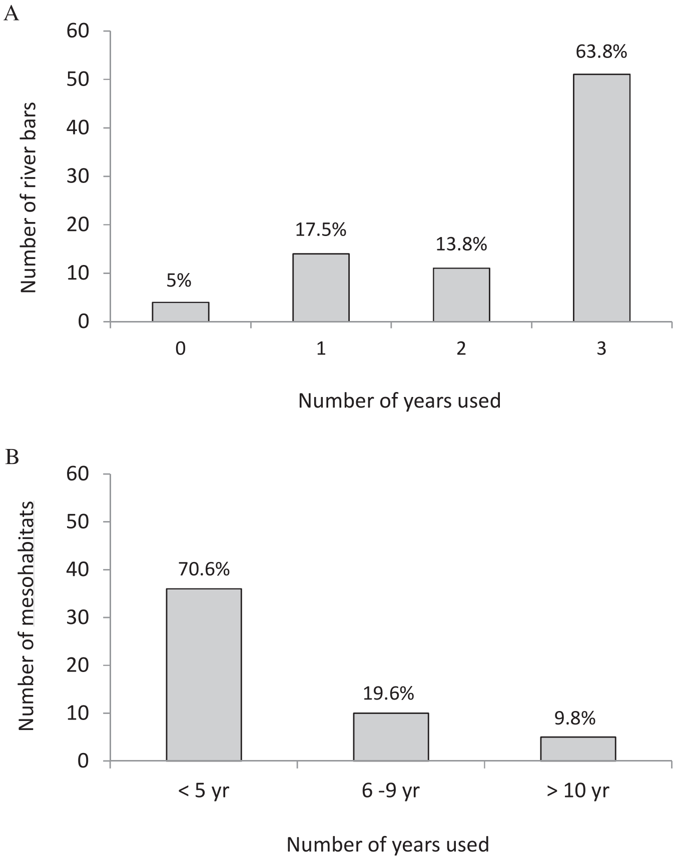

FIG. 5. *Rana boylii* breeding area use of (A) South Fork Trinity River stream bars for 80 bars surveyed from 1992 to 1994, and (B) Hurdygurdy Creek stream mesohabitat units for 51 mesohabitats surveyed from 1987 to 2002. Numbers above each bar are the percentage of stream bars/mesohabitat units for each year category.

Relative Abundance and Breeding Area Use.—Egg mass relative abundances were consistently high at the South Fork Trinity River and Hurdygurdy Creek localities and were substantially higher (19–47/km) compared with the Main Fork Trinity (<1–1.7/km; see table 1 in Lind et al., 1996). The Main Fork Trinity River site was located downstream of a dam and the amount of potentially suitable breeding habitat was very limited compared with the other two localities as a result of altered environmental conditions in this highly regulated river (Lind et al., 1996).

Egg mass counts do not provide a direct measure of reproductive success, but these data are a useful metric in assessing habitat quality (Resetarits, 1996; Baldwin et al., 2006). The models that best explained egg mass relative abundance at the South Fork Trinity River included distance from shore and water depth as key variables. Together these variables were indicative of wide, shallow areas as prime breeding sites for frogs and areas that can accommodate large numbers of egg masses and ultimately tadpoles. These shallow habitats also may provide optimal thermal conditions conducive to embryonic and tadpole development, and higher algal food abundance (Catenazzi and Kupferberg, 2013; Wheeler et al., 2014). We acknowledge that our method of data collection was not rigorous and our estimates of egg mass relative abundances may have been biased because we did not assess detection probabilities to adjust for the proportion missed (Campbell Grant et al., 2005). Although the results were not unexpected to us given our extensive knowledge of the species, we admit that there may be limitations to their interpretation.

Much of the work on amphibian site fidelity has focused on species that use lentic environments (e.g., Reading et al., 1991; Sinsch, 1992; Hels, 2002), but amphibians also differentiate between suitable and unsuitable habitat in continuous lotic environments (Crump and Pounds, 1989; Joly and Miaud, 1989). Repeated use of the same bar or mesohabitat unit over many years indicates that adults probably return to the same areas to breed each year and their offspring also may use these areas. Some sites along Hurdygurdy Creek were used years beyond the species' suspected life expectancy. At one such breeding hot spot, some males were recaptured over two to four reproductive seasons and females were recaptured over two to three seasons; one female was initially captured in 2002 and recaptured in 2003 and 2008 (CAW, unpubl. data). At this particular breeding hot spot at Hurdygurdy Creek, an average of 26 egg masses was found per year over the 16 yr surveyed. Breeding aggregations such as these may increase the likelihood that more individuals will successfully find mates (Wells, 1977). Survival rates of tadpoles are likely enhanced in these areas because of optimal conditions of temperature and food availability even with increased competition from conspecifics (Kupferberg, 1997a,b). Individual predator risk would be reduced with faster developmental rates and as a consequence of being in a large aggregation (Wilbur, 1980). Furthermore, use of shallow water environments could reduce predation by some (salmonid fishes and Pacific giant salamanders, *Dicamptodon tenebrosus*) but not all (garter snakes and wading birds) predators.

Implications for Conservation and Management.—*Rana boylii* is declining in some areas of its geographic range, with suspected factors being habitat alteration (especially hydrologic changes resulting from dams) and alien predators/competitors (Jennings and Hayes, 1994; Kupferberg 1996, 1997a; Lind et al., 1996, 2003; Davidson et al., 2002; Lind, 2005). Our abundance data from relatively robust populations in the northern Coast Range (Fig. 3) provide baseline information and target recovery population sizes for areas where *R. boylii* is declining.

Streams are extremely dynamic systems with disturbance regimes that span a large range of temporal and spatial scales (Townsend and Hildrew, 1994; Allan, 2000). Stream fauna experience frequent small-scale (annual winter/spring high flows) and less frequent large-scale flood (10–20+-yr recurrence) disturbances that change their environment through transport and deposition of substrates, shifting in channel positions, and reordering of mesohabitat units (Frissell et al., 1986; Trush et al., 2000). Annual disturbances may alter conditions (e.g., water depths and velocities) for *R. boylii* at the scale of oviposition sites and require local (on the order of meters) shifts in habitat use; whereas large-scale flood events could result in relocation of *R. boylii* breeding areas to newly created stream mesohabitat units, bars, or channels. Repeated use of the same gravel bar or mesohabitat units as seen in this work is an indication that breeding habitat selection is occurring not just at the microscale, but at larger spatial scales. The effectiveness of management in meeting conservation objectives may be improved by protecting breeding hot spots (including sections upstream and downstream of hot spots to allow for shifts that may result from disturbance events) and maintaining the fluvial processes that produce them.

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