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Demography, Habitat, and Movements of the Sierra Nevada Yellow-Legged Frog (*Rana sierrae*) in Streams

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The Sierra Nevada Yellow-Legged Frog (*Rana sierrae*) has generally been viewed as a lake species, but it has increasingly been found in streams, including in the northern part of its range where it is particularly at risk. Developing effective conservation strategies has been hindered by a lack of knowledge of its basic ecological requirements in stream habitats. To address this information gap, we investigated the demography, habitat use, and movements of stream populations of this federally endangered species. We conducted capture–mark–recapture of adults, quantitatively described stream channel and riparian vegetation characteristics, and collected habitat use data at four northern Sierra Nevada mountain streams, counted egg masses at three central Sierra Nevada streams, and radio-tracked individuals at three central and southern Sierra Nevada streams. Stream populations in the northern range were very small with maximum abundances of <15 individuals, and apparent survival probability ranged from 0.57–0.81. In contrast, one southern Sierra Nevada stream had a large count of 547 adults. Egg mass counts ranged from 22–104 per stream. We found frogs in diverse headwater streams ranging from perennial to intermittent flow regimes, pool versus riffle dominated, and low to high channel gradient, and they used diverse microhabitats within these streams. In these stream habitats, frogs moved little over four-day survey periods but were capable of moving longer distances of up to 1248 m over the summer. Conservation and management of the at-risk *R. sierrae* are most likely to be effective when built on comprehensive quantitative information on basic ecological requirements in all habitats used by the species.

EFFECTIVE management to conserve declining or endangered species relies on comprehensive and accurate information on an organism's basic ecological requirements (Carroll et al., 1996; CDFW, 2012; Murphy and Weiland, 2016). Understanding ecological requirements for all life stages (Bull, 2009), across all seasons (Fellers and Kleeman, 2007; Pearl et al., 2018), and for all types of habitats used by a species (Browne et al., 2009; Fellers et al., 2013) can increase the likelihood of a more successful, sustainable recovery. In the absence of such comprehensive information, decisions may be based on narrow assumptions about habitat use and other requirements gleaned from general knowledge, expert opinion, and the few published studies that exist (Sutherland et al., 2004). Using such incomplete information may be costly and lead to poor decisions when, lacking information, we assume a species behaves one way universally or we ignore all habitats in which it is found. Quantitative data that describe demography, habitat relationships at multiple scales, reproduction ecology, and behaviors such as movement lead to more comprehensive conservation and management decisions for endangered species across multiple taxa (Dodd and Seigel, 1991; Lantz et al., 2007; Fellers et al., 2013; Klinger et al., 2015; Lind et al., 2016; Pearl et al., 2018). Such information can provide a fuller view of the breadth of a species' realized niche.

The federally endangered Sierra Nevada Yellow-Legged Frog complex (*Rana sierrae, Rana muscosa*) has generally been considered a lentic species where it has been relatively well studied, particularly in high alpine lake habitats in the central and southern Sierra Nevada mountains (e.g., Bradford, 1984; Knapp et al., 2003; Matthews and Preisler, 2010; Vredenburg et al., 2010). Once historically abundant in the Sierra Nevada (Grinnell and Storer, 1924), *R. sierrae* has declined in distribution and abundance (Vredenburg et al., 2007; Brown et al., 2014a). Although it is now rare in most of its range, historically, populations of hundreds of frogs have been reported for lakes in high alpine areas in the central and southern Sierra (Bradford, 1991; Vredenburg et al., 2010; Brown et al., 2014a). The species is highly aquatic, but its use of aquatic habitats may differ across its range. Based on knowledge from the central and southern Sierra Nevada, larvae take two to three years to metamorphose and thus require permanent water that does not freeze over winter to survive (Zweifel, 1955; Bradford, 1983). Thus, the more well-known habitats used for breeding are deep lakes (Knapp and Matthews, 2000; Knapp et al., 2003). During nonbreeding periods in alpine areas in the central and southern Sierra, frogs move among a larger variety of aquatic habitats for feeding, including more ephemeral sites that may be unsuitable for overwintering or breeding. They then tend to return to the same places to breed and overwinter (Pope and Matthews, 2001; Matthews and Preisler, 2010).

In contrast to its lake ecology, little is known about the ecology of *R. sierrae* in streams (Brown et al., 2014b; MYLF ITT, 2018). To our knowledge, with the exception of one creek in its southern range, few large populations have been reported for streams. But, this may be due to lack of information. Biologists report finding the occasional frog while conducting stream surveys, but, in general, their densities do not appear to reach those commonly reported from lake environments. It remains unknown whether abundances are low or whether the species' ecology differs in streams resulting in more dispersed populations. For example, remaining populations in the northern range are thought to be primarily in streams (MYLF ITT, 2018). In this

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region, only a few breeding sites have been found and these differ markedly from the lakes where the species has historically been studied. Indeed, little is known about the species' breeding ecology throughout its range. Finally, to date, virtually nothing is known about movements or habitat affinities of *R. sierrae* in streams.

To address these knowledge gaps, we studied populations of *R. sierrae* in stream habitats to examine assumptions of what we know about this species that ostensibly depends on lentic environments. Our objectives were to (1) quantify population abundance and other demographic parameters in streams, (2) investigate egg-laying behavior such as the degree of communal breeding, (3) quantify the general types of streams and specific microhabitats used by *R. sierrae* including the types of habitats where *R. sierrae* lay their eggs, (4) quantify frequency, distances, and patterns of adult movements, and (5) quantify levels of infection by the amphibian chytrid fungus, *Batrachochytrium dendrobatidis* (*Bd*). We evaluated both similarities and differences in these aspects of the ecology of *R. sierrae* in streams compared with what is generally known for those inhabiting lakes. This study contributes to recovery of *R. sierrae* by quantitatively extending our knowledge on the demography, ecology of breeding site selection, habitat use, and movements of this federally endangered species in a habitat type where it has not typically been studied.

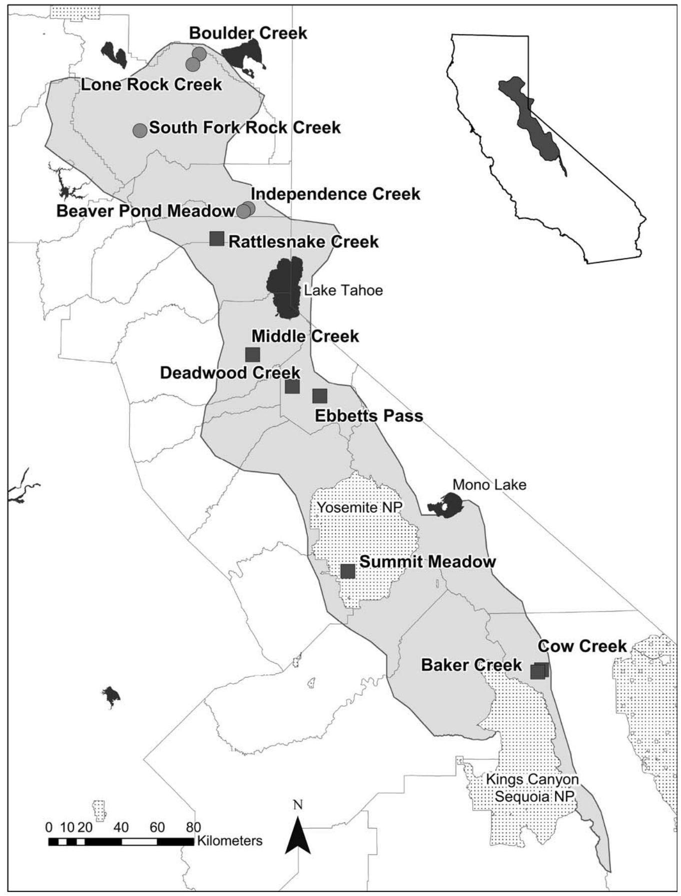

Fig. 1. Locations of sites of *Rana sierrae* surveyed in 2003 and 2009–2011. The shaded area shows the range of *Rana sierrae*. Squares are 2003 survey streams and circles are 2009–2011 survey streams. County lines are shown for reference.

MATERIALS AND METHODS

Study streams

We counted egg masses and collected habitat data at egg mass locations in spring 2003 at five streams including Deadwood Creek, Ebbetts Pass, Middle Creek, Rattlesnake Creek, and Summit Meadow in the north-central portion of the species' range, encompassing a variety of habitats (Fig. 1, Table 1). We collected demography, habitat, and movement data from 2009–2011 at four streams in the northern portion of the species' range including Independence Creek (length = 1556 m), Lone Rock Creek (length = 1390 m), South Fork Rock Creek (length = 2407 m), Boulder Creek (length = 1265 m), and one meadow near Independence Creek (referred to as the Beaver Pond meadow) as part of a three-year monitoring program. In 2003, we collected movement data using radio-telemetry at three streams (Baker Creek, Cow Creek, and Deadwood Creek) in the central and southern portion of the species' range. We selected sections of the streams to survey based on known occupancy resulting from prior survey efforts and, for the 2009–2011 streams, based on forest management priorities.

Field methods

Population surveys.—In 2003, we conducted egg mass surveys at snowmelt toward the end of breeding from May–June, including walking shorelines and snorkeling along the edges of streams. We surveyed streams, meadows, and complexes of stream, meadow, and lake habitats. In each stream, we surveyed the entire reach where we found eggs or frogs, plus 2 km up- and downstream past the last point where we found the species. In some cases, the stream changed character to higher gradients such as waterfalls, emptied into lakes, or simply ended. We recorded counts of masses and, for each egg mass, we measured the diameter of the egg mass to describe morphology and the distance to the nearest conspecific egg mass to quantify the degree of clustering. We measured the longest diameter of egg masses for those that had not been disturbed and were found after jelly had stabilized and before disintegration just before hatching. We recorded counts of frogs during egg mass and radio-tracking surveys. Counts generally underestimate abundance compared with capture–mark–recapture estimates (CMR), but they can provide baseline information on magnitudes of population size.

In 2009, 2010, and 2011, we conducted CMR surveys for adult *R. sierrae* the third week in August using a robust design (Pollock, 1982). For each year (primary period), we surveyed each stream on four consecutive days (secondary period) for at least six hours per day between 0930–1730 hrs. We also conducted a spring survey for three consecutive days in June 2010 at Independence Creek. We searched all aquatic habitats within the vicinity of each study reach, including the channel itself, mouths of tributaries, backwaters, side channels, and adjacent meadow habitat.

We recorded sex, length, mass, and capture location coordinates of each frog. We collected tissue swabs from a subset of frogs to test for the presence of *Bd* (Boyle et al., 2004; Frías-Alvarez et al., 2008). We PIT-tagged all unmarked frogs >40 mm snout–urostyle length using AVID MUSICC Microchips^{TM} (Heyer et al., 1994; Pope and Matthews, 2001).

Habitat surveys.—In 2003, at each egg mass we collected habitat data at two scales. First, we recorded the substrate used for attachment, the depth of the egg mass, the distance

Table 1. Years surveyed and data collected at study streams of *Rana sierrae* in 2003 and 2009–2011.

		Data collected							
		Population			Movement		Habitat		
Stream	Years surveyed	CMR	Counts	Egg mass	Pit tags	Radio-tracking	Site	Adult	Egg mass
Deadwood Creek	2003		X	X		X			X
Ebbetts Pass	2003			X					X
Middle Creek	2003		X	X					X
Rattlesnake Creek	2003		X	X					X
Summit Meadow	2003			X					X
Cow Creek	2003		X			X			
Baker Creek	2003					X			
Independence Creek	2009–2011	X	X		X		X	X	
Beaver Pond Meadow near Independence Creek	2009–2011	X	X						
Lone Rock Creek	2009–2011	X	X		X		X	X	
South Fork Rock Creek	2009–2011	X	X		X		X	X	
Boulder Creek	2009–2011		X		X		X	X	

from the top of the egg mass to the surface of the water, and the depth from the bottom of the egg mass to the bottom of the stream, lake, or pond. Second, at each location where we found clusters of egg masses, we measured in-stream characteristics including depth, flow, bank angle, canopy cover, stream gradient near the egg masses, and water temperature, as well as stream morphology, including bankfull width, wetted width, depth at thalweg, and stream gradient over a longer stream section.

From 2009 to 2011, we collected habitat data for all frogs at two scales. First, in 2009, we collected reach-scale habitat data to describe general characteristics of the study streams. Reach scale data included channel gradient, habitat unit type (e.g., pool, run, riffle), bankfull width, wetted width, pool water depth, residual pool depth, percent of fine sediment (<2 mm) in pool tails, stream shading (% canopy cover) using a Solar Pathfinder®, and classification of riparian hardwood age structure (USFS, 1996; CDF&G, 1998). We collected maximum water depth, residual pool depth, and percent of fine sediment (<2 mm) at each pool. Second, in 2009, 2010, and 2011, we collected microhabitat data at the site where individual frogs were encountered during population surveys. We collected microhabitat data at each frog locality the first time an individual frog was found each day. We collected microhabitat data again if the same frog was found >4 h since its last sighting. We described 1) the general habitat, including location relative to the stream (e.g., in stream, on shore, backwater), habitat unit type (e.g., pool, run, riffle), and distance to shore or water, 2) stream size, including water depth and wetted width, 3) cover in a 1 m^2 plot around the frog including dominant substrate and percent of cover for different cover types (herbaceous, woody, woody debris, and total cover), and 4) stream shading (% canopy cover) at the frog's location. Total cover included any type of cover in which a frog could hide, such as silt or cobble substrate, vegetation, or woody debris.

Radio-tracking.—In 2003, we used radio telemetry to study the habitat use and movements of post-metamorphic frogs. We attached compact radio-transmitters (Holohil BD-2 transmitters) to adult frogs with beaded belts (Rathbun and Murphey, 1996). Radios were attached 2–6 weeks after breeding, depending on access to the stream. We tracked the frogs approximately every 14 d, recording coordinates of each sighting using a Garmin handheld GPS unit. The crew made every effort to find animals with transmitters, searching up to two hours and up to 300 m upstream and downstream beyond the last known point where a frog was found. Radio-transmitters can detect locations up to several km. If the frog was not found, we assumed the radio transmitter had died.

Data analysis

Abundance and survival.—For egg masses found during the 2003 surveys, we tallied number of locations at each stream where egg masses were found and total counts of egg masses. We also used the descriptive statistics, mean, standard deviation, minimum, and maximum, to summarize the size of egg masses and degree to which they were clustered based on distance to the nearest egg mass. For other life stages found during 2003 surveys, we reported the number found per survey.

For 2009–2011 surveys, where sample sizes were sufficient, we analyzed capture–mark–recapture data to estimate abundance and apparent survival of adults at each study stream using Pollock's robust design (Pollock, 1982). We validated the closure assumption for each stream/year by comparing a Pradel model (Pradel, 1996) with no immigration (recruitment = 0, closed model) to a model allowing immigration (recruitment unconstrained, open model; Boulanger et al., 2002). The closed and open models for each stream and year were compared using likelihood ratio tests. In all cases, the closed model had the most support or there was no difference between the models, indicating the closure assumption was valid. To reduce the number of models for comparison, we conducted exploratory analyses for each stream/year by fitting the data to four Huggins closed population models where the probability of capture was held constant (M_o) or allowed to vary by behavior (M_b), time (M_t), or both (M_{tb}; White et al., 1982). For each stream, we chose the closed population model that had the most support based on Akaike weights (w_i) using $QAIC_c$ values for inclusion in the robust design analysis. We fit the data to 12 models using Pollock's robust design model where 1) apparent survival (Φ) was held constant or allowed to vary among years, 2) the probability of capture (p) and recapture (c) were modeled with the most supported closed population model and were either held constant or were allowed to vary among years, and 3) temporary emigration (G) was either none (frogs did not skip years), random (frogs presence was random), or Markovian (the probability of the frog's presence at the aggregation was dependent on its presence the prior year). We used the program RDSurviv (Kendall and Hines, 1999) to test the goodness of fit for the most general model for each stream and to calculate the variance inflation factor, $\hat{c}$, based on the Pearson's χ^2 test ($\hat{c} = \chi^2$/df; Amstrup et al., 2005). Model selection was based on Akaike weights (w_i) calculated from $QAIC_c$ values (Burnham and Anderson, 2002). Some models could not be fit to the data or had unreasonable parameter estimates and were dropped from the final model set. Final estimates were calculated by model averaging the final set (Burnham and Anderson, 2002). Model fitting and averaging were conducted using the R (R Development Core Team, 2009) package RMARK (Laake, 2010).

At the Beaver Pond meadow (near Independence Creek), where only two years of mark–recapture were conducted, we analyzed the mark–recapture data for *R. sierrae* using Huggins closed capture models in program MARK (White and Burnham, 1999). We fit the data to four models where the probability of capture was held constant (M_o) or allowed to vary by behavior (M_b), time (M_t), or both (M_{tb}; White et al., 1982). Some models could not be fit to the data or had unreasonable parameter estimates and were dropped to form a final model set. This final model set was then used to calculate population and parameter estimates by model averaging (Burnham and Anderson, 2002).

At Boulder Creek, sample sizes were insufficient for mark–recapture analysis, and we report only the number of unique individuals detected. Because larvae and most subadults could not be marked individually with PIT tags, CMR analysis was not possible for these life stages. To provide a conservative population index that minimizes doubly counting individuals, we report the maximum number of individuals observed in a single day.

Distance traveled and spatial distribution from population surveys.—We investigated the distance traveled by frogs both within each four-day CMR period and among years. We combined the June and August surveys at Independence Creek in 2010. We calculated straight line distance between each pair of consecutive frog locations. Because individuals were captured multiple times during a single year, we selected the last capture date in each year as a representative position to calculate distance moved among years. To investigate the spatial distribution of frogs along each stream, we mapped each frog location by life stage for each year and visually examined the patterns.

Distance traveled and movement patterns based on radio-telemetry.—We investigated the pattern and distances of radio-tracked frog movements along the streams. We first calculated the distances each frog moved along the stream between each pair of consecutive capture locations. We then calculated the proportion of times each frog moved between surveys. Using only data where frogs moved, for each frog, we calculated the average distance moved between captures, the maximum distance traveled between captures, and the total distance moved over the study period (sum of all movements). Finally, we calculated summary statistics for each stream.

Habitat.—We examined the 2003 habitat data for egg masses using descriptive statistics (mean, standard deviation, minimum, and maximum), at both the general locations with egg masses (i.e., multiple masses may have been found here) and at each egg mass location. For the 2009–2011 surveys, we examined the available habitat at the reach-wide scale within the survey stream and microhabitat associations of *R. sierrae* with the same descriptive statistics. For overall frog habitat associations and comparisons by sex, only data for marked adults on the four primary study streams were used. Our methods were less appropriate for the more lentic Beaver Pond meadow. To examine the influence of multiple captures of the same frog, we randomly selected one capture per individual. Because results were similar, our summaries here include data for all captures. We used all data on adults and subadults to compare habitat use between life stages. We provide descriptive narratives for tadpole locations since few were found.

RESULTS

Abundance and survival.—Populations were small at all streams surveyed in 2009–2011 (Table 2), ranging from only a few individuals at two streams to an estimated 6–13 frogs at Lone Rock Creek. The Beaver Pond meadow had the largest estimated population size with 35.8 males (SE = 6.30) and 32.7 females (SE = 5.88) in 2011. At two streams, population estimates decreased somewhat each year. At Independence Creek, the population estimates from June 2010 were larger than those in August of each year. Tadpoles were detected at three of the four study streams and at the Beaver Pond meadow. Multiple age classes of tadpoles were found at two of these streams and the Beaver Pond meadow.

Sex ratios varied among streams. The proportion of males ranged from 0–0.52. In all sites except the Beaver Pond meadow, females were more abundant than males. Only females were detected in some years at most streams. Annual survival ranged from 0.57–0.81 at the three streams where it could be estimated (Table 2). At Independence Creek, models with time-dependent survival could not be parameterized so survival estimates were constant across all sample periods. At the other two streams, model averaged survival estimates were similar among years. Probability of detection ranged from 0.38–0.55.

Population counts were similarly small for streams surveyed in 2003, with the exception of Cow Creek, located in the southern part of the species' range, where 547 adults were counted (Table 3). Counts of frogs at Deadwood Creek were larger than the northern stream populations, but were still relatively small with a maximum count of 34 adults.

Egg masses.—In 2003, we found 225 egg masses ranging from 22–104 per stream (Table 3). Multiple egg masses tended to be laid in the same general areas, though they were not usually clumped on top of each other. Eggs were found in 2–6 locations per stream spaced approximately 5–300 m apart, with a median of four masses per location. The maximum number of masses found in one place was 67 in a small inlet stream. The median linear distance between masses per stream ranged from 0.02–0.27 m (Supplemental Table 1; see Data Accessibility). Average diameters of egg masses varied from 5.3–14.8 cm. We found more egg masses than adults in two of the three streams that had both egg mass and frog counts.

Table 2. Summary of population and survival estimates for *Rana sierrae* at streams surveyed 2009–2011. Model averaged population estimates for adults of *R. sierrae* at Independence Creek, Lone Rock Creek, and South Fork Rock Creek are from robust design methods and are shown with standard error in parentheses. For Boulder Creek, adult counts are the number of unique tagged individuals; no frogs were found at the primary stream reach in Lowe Flat. For the Beaver Pond meadow near Independence Creek, 2009 adult counts are numbers of unique tagged individuals, and model averaged population estimates of adults in 2010 and 2011 are from Huggins closed capture methods and are shown with standard error in parentheses. Subadult and larvae counts are the maximum number observed on a single day. No surveys were conducted at Boulder Creek in 2009 and spring surveys were only conducted at Independence Creek in June 2010.

Site	Metric	Life stage	2009	June 2010	Aug 2010	2011
Independence Creek	Population estimate	Adult male	0	2.4 (0.7)	3.2 (0.52)	3.2 (0.43)
		Adult female	2.4 (0.93)	7.1 (1.34)	3.2 (0.52)	5.3 (0.58)
	Survival	Adults			0.81 (0.2)	0.81 (0.2)
	Maximum count	Subadult	27	5	17	8
		Larvae	76	0	68	50
Beaver Pond Meadow near Independence Creek	Population estimate	Adult male	2	No	8.5 (2.4)	35.8 (6.30)
		Adult female	2	Survey	9.9 (2.67)	32.7 (5.88)
	Maximum count	Subadult	29		74	28
		Larvae	5		55	96
Lone Rock Creek	Population estimate	Adult male	2.3 (0.55)	No	2.2 (0.49)	0
		Adult female	11.3 (1.35)	Survey	6.6 (0.9)	6.3 (1.8)
	Survival	Adults			0.78 (0.25)	0.74 (0.28)
	Maximum count	Subadult	3		7	9
		Larvae	0		7	8
South Fork Rock Creek	Population estimate	Adult male	3.1 (0.37)	No	1.0 (0.14)	0
		Adult female	1 (0.21)	Survey	2.0 (0.20)	2.1 (0.41)
	Survival	Adults			0.57 (0.22)	0.61 (0.25)
	Maximum count	Subadult	1		0	0
		Larvae	0		0	0
Boulder Creek	Population counts	Adult male	No	No	0	0
		Adult female	Survey	Survey	2	1
	Maximum count	Subadult			5	4
		Larvae			0	1

Available habitat.—At the reach scale, the four 2009–2011 study streams contained diverse habitat structure (Fig. 2, Supplemental Table 2; see Data Accessibility). All four streams were relatively small, low (first to third) order streams. Average bankfull widths ranged from 2.9–4.2 m. Three streams were predominantly low gradient response type channels (averages ranging from 1.1% to 3.7%), whereas South Fork Rock Creek averaged 8% and functioned more as a transport type channel. South Fork Rock, Lone Rock, and Boulder creeks had both low and high gradient sections. Two of the streams, Independence Creek and Lone Rock Creek, were perennial, whereas two, South Fork Rock Creek and Boulder Creek, became intermittent later in the summer, drying to only a few pools. South Fork Rock Creek was the most intermittent, and by October, wetted widths dried to an average of 19% of bankfull widths. In this stream, 62% of the 69 habitat units in 2009 and 57% of the habitat units in 2011 were dry by October.

Available habitats varied from pools that dominated Lone Rock and Boulder creeks to almost all riffles at South Fork Rock Creek (Fig. 3). Independence Creek had more riffles but also had pools and runs. Although the number of pools was similar among reaches, the proportion of the habitat composed of pools varied, ranging from 8–58% (Fig. 4). Maximum and residual pool depths were higher in Lone Rock and Boulder creeks indicating deeper pools (Fig. 2, Supplemental Table 2; see Data Accessibility), though all were shallow relative to high mountain lakes where *R. sierrae* has generally been studied in the past. Lone Rock and Boulder creeks had high levels of pool tail fines, whereas Independence Creek was lower than expected for a meadow response reach.

Independence Creek had numerous braided channels flowing through a meadow. Sections of Lone Rock Creek flowed through downcut dry meadows, and there were localized sections with herbaceous vegetation along stream edges on all four reaches. Riparian vegetation consisted of willow (*Salix* spp.) and alder (*Alnus* spp.) in three of the streams, whereas only conifers were found in South Fork Rock Creek. Aspen was found in Independence, Lone Rock, and Boulder creeks. Shade was moderate, averaging 33–55% among the streams.

In Boulder Creek, we collected habitat data along a 1,265 m reach that has historical sightings of *R. sierrae*. However, the few frogs observed during our surveys were found above this designated study reach. The section of Boulder Creek where we found frogs contained water intermittently with sections of both flowing and pooled water with observable turbidity. The majority of the stream reach was low to moderate gradients with organic and vegetative substrate, with one steep boulder field where water flowed sub-surface. In most sections of this reach, the stream channel was generally narrow with dense vegetation dominated by willows intermixed with alders. Canopy openings above the stream occurred in very small forested sections or directly upstream of beaver dams where the stream had been modified into large flooded wetlands.

Table 3. Summary of egg mass, adult, subadult, and tadpole counts and general description of egg mass habitat for *Rana sierrae* at streams surveyed in 2003. Egg masses were clustered in multiple locations. Counts of adults, subadults, and tadpoles were collected at the scale of the entire stream.

			Egg masses					Other life stages			
Site	Description of egg mass habitats	Type of habitat	Dates surveyed	# Locations	# Masses	Median # masses/ location	Range # masses/ location	Dates surveyed	# Adults	# Subadults	# Tadpoles
All sites				22	225	4	1–67				
Deadwood Creek	Egg masses were found in stream and in marshy areas feeding into stream.	Total for stream	7/10–7/11	5	34	5	4–13	6/20	9	1	1
								7/10	28	19	515
								7/24–7/25	34	26	56
		Oxbow ponds		4	30	5.5	4–13				
		Stream		1	4	4	4				
Ebbetts Pass	Egg masses were found in inlet creek to small pond and in the pond.	Total for stream	6/25–6/26	3	104	34	3–67	No data			
		Inlet		2	101	50.5	34, 67				
		Pond		1	3	3	3				
Middle Creek	Egg masses were found in the channel.	Total for stream	6/8–6/9	6	27	3	3–9	6/8–6/9	12	10	3
Rattlesnake Creek	Egg masses were found in a small off-channel pond that is seasonally connected to creek.	Total for stream	6/14	2	22	11	7, 15	6/13	6	0	0
								6/15	9	2	58
Summit Meadow	Egg masses were found in the main stream and in adjacent marshy areas feeding into stream.	Total for stream	6/23–6/24	6	38	2.5	1–28	No data			
Cow Creek								8/11	547	178	330

Beaver activity occurred in three of the four watersheds and was most pronounced in the lower sections of Lone Rock Creek. In the study reach of this stream, the number of beaver dams increased from four in 2009 within about the lower 150 m of the reach to 13 in 2010 and 12 in 2011 scattered through approximately the lower 1000 m of the reach. Nearby Boulder Creek also had signs of beaver. Finally, although no signs of beaver were observed on our Independence Creek study reach, evidence of beaver were present within this watershed. This includes the large Beaver Pond meadow with a complex of habitats that ranged from deep pools to shallow flooded vegetation. While most of this meadow had an open canopy, wetted habitat on the margins was shaded by mature conifers and aspen, and large (2.4–3.7 m high) willow shrubs occurred throughout the meadow. Frogs were found in many types of habitats in this meadow, including two of the channel outlets. One was a small, medium-gradient stream with rocky substrate that included a mix of boulders, cobble, and gravel. The other was a small, silty, medium gradient stream.

For the 2003 streams, we provide qualitative descriptions since we do not have the same quantitative data for these sites. The 2003 streams were also low-order small headwater systems. Middle and Rattlesnake creeks were most like the later study streams. Several of the 2003 streams had more lentic types of habitats, and multiple sites had a heterogeneous mix of habitats. Ebbetts Pass was a small inlet stream that flowed into a lake. Deadwood Creek had a deep and slow-moving channel, marshy floodplains, off-channel ponds, and a steeper, more rocky section. Baker Creek also had a deep slow-moving channel with a marshy floodplain. Deadwood Creek, Summit Meadow, Baker Creek, Cow Creek, and Ebbetts Pass all had marshy sections of the creek and

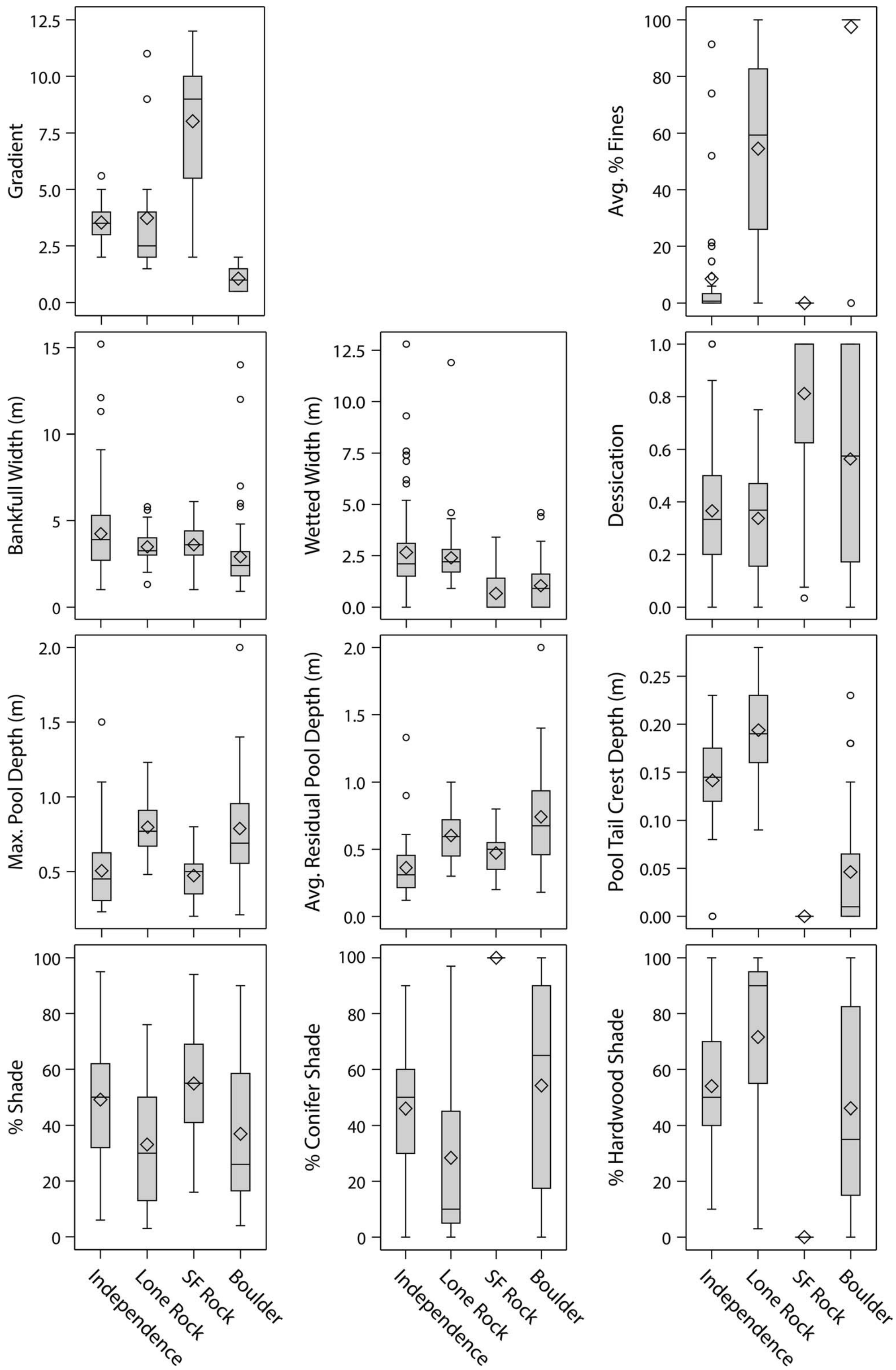

Fig. 2. Summary of reach-wide available habitat based on inventories for each survey stream of *Rana sierrae*, 2009–2011. Diamonds are averages and horizontal lines in center of boxplots are medians. Dessication = 1-wetted width/bankfull width. On South Fork Rock Creek, because channel conditions were primarily dry during the time that the habitat inventory was completed, assessment of pool tail crest depths and percent pool tail fines was not possible. Supplemental Table 2 provides these data in tabular format (see Data Accessibility).

floodplains. Rattlesnake Creek was intermittent with dry sections later in the summer.

Fishes occurred throughout Independence and Lone Rock creeks, and the lower portions of Boulder and South Fork Rock creeks. Although stranded fishes were occasionally found in South Fork Rock Creek, its intermittent water prevented fishes from regularly inhabiting the entire reach. At Boulder Creek, the steep boulder field with sub-surface water prevented fishes from reaching the upper section where frogs were found. Introduced trout (*Oncorhynchus mykiss*) were also found in Baker Creek.

Used habitat.—More than half (67%) of the marked adult frog captures were in the streams, 18% were on shore, and 15% were in backwaters, tributaries, or side channels. The latter were found at Independence Creek, the braided stream system in a meadow with numerous spring-fed tributaries and side channels. Most of the frogs found in these habitats were in water. At Independence Creek and Lone Rock Creek, subadults also were found in backwaters, tributaries, and side channels. Combining streams, 46% of marked adult frog captures were in pools, 16% in runs, and 33% in riffles, but the pattern differed among reaches. Frogs appeared to select

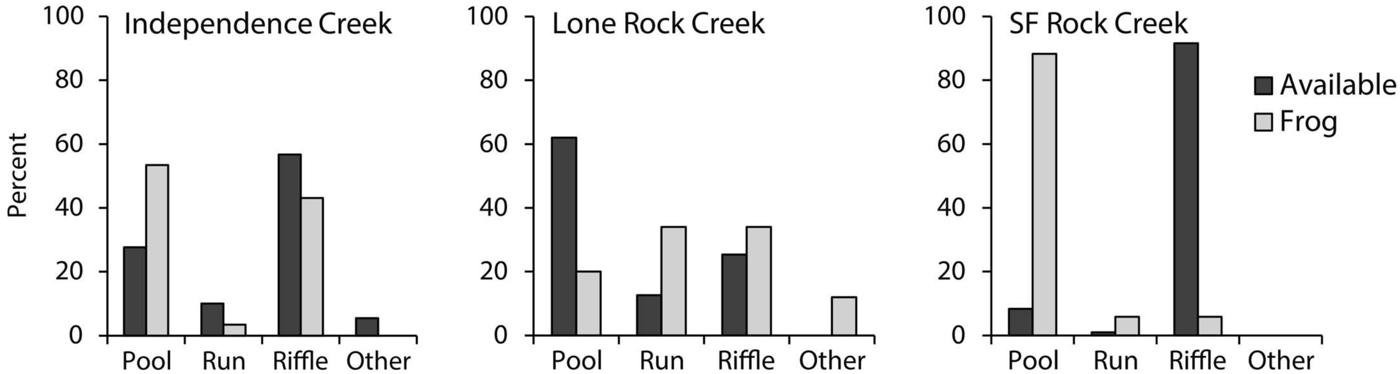

Fig. 3. Comparison of habitat types used relative to available by marked adults of *Rana sierrae*, 2009–2011. Available is the average of percentages of stream length measured in 2009 and 2011. Frog usage is the percent of all captures. Differences in habitat usage were significant at Independence Creek, South Fork Rock Creek, and Lone Rock Creek (chi-squared test, alpha < 0.05).

pools more often relative to the available habitat at Independence Creek and South Fork Rock Creek (Fig. 3). The few frogs found at Boulder Creek also were found in pools. At Lone Rock Creek, pools were the dominant habitat, but frogs were found more often in runs and riffles. At Lone Rock Creek, 62% of subadults were found in pools, but no differences were found at the other reaches. Marked adult frogs were found within 1 m of water (maximum distance $=$ 0.5), and when in water, were found an average of 0.4 m from shore (sd $=$ 0.7, maximum $=$ 4.5 m, Fig. 5, Supplemental Table 3; see Data Accessibility). The average water depth where marked adult frogs were found was 0.1 m (sd $=$ 0.10), but the median was half that at 0.05 m; the maximum was 0.8 m. The average wetted width was 3.4 m (sd $=$ 2.3) with a maximum of 11 m. The average shade where frogs were captured was 56% and ranged from 18–98%.

When in the streams, marked adult frogs were generally found at locations with total cover averaging 52% (range $=$ 0–100%; Fig. 5, Supplemental Table 3; see Data Accessibility). A large portion of this cover was provided by channel substrate. Frogs were generally found in areas dominated by silt (19% of captures), cobble (33%), or boulders (23%). Streams in general had low herbaceous cover and frogs found in water were generally found in areas averaging 14% herbaceous cover (range $=$ 0–100%). Frogs found in water also were found in areas with low shrub (average $=$ 20%, range $=$ 0–100%) and woody debris (average $=$ 9%, range $=$ 0–80%) cover. When on shore, marked adult frogs were found in areas with an average of 59% total cover (range $=$ 10–100%). Silt was the most common substrate (45% of captures), and frogs were found in areas with an average of 30% herbaceous (range $=$ 0–90%), 22% shrub (range $=$ 0–100%), and 10% woody debris cover (range $=$ 0–50%). In addition, subadults were found more often in stream areas with silt, whereas adults were found more often in cobble and boulders. Otherwise, with a few exceptions noted above, no differences were found in habitat use between adults and subadults or between males and females.

Tadpoles were found in a variety of habitats. At Independence Creek, tadpoles were found in two areas. The primary area with tadpoles all three years was a small spring-fed tributary with gravel and cobble substrate and a maximum width of about 1 m. Water depths in August were only about 0.1 m in most areas, with a maximum depth of about 0.3 m. In 2009, tadpoles were also found in pools in a side channel with cobble substrate, little vegetation, and a maximum depth of about 0.3 m. There was little to no flow in this area because of a gravel bar that cut off the flow from the main channel. At Lone Rock Creek, tadpoles were found in a shallow (approximately $<$0.2 m) flooded area with tall grassy vegetation at the edge of the stream. The adjacent channel was deep ($>$1 m). This flooded area was not present in 2009 and was probably created by a beaver dam about 10 m downstream. Finally, at Boulder Creek, the lone tadpole was found in a shallow grassy side pool outside the main flow just downstream from a beaver dam.

Egg mass habitat.—Egg masses tended to be located in a wide variety of habitats. Egg masses were found in the stream and in marshy areas feeding into the stream at Deadwood Creek and Summit Meadow. At Ebbetts Pass, we found egg masses in the inlet creek to a small pond and in the pond. At Rattlesnake Creek, we found egg masses in a small seasonally connected off-channel pond, and at Middle Creek, we found egg masses in the main stream channel.

Attachment sites varied by habitat type (Fig. 6). In creek habitats, the majority of eggs were attached to rock substrate, with the remaining attached to wood, vegetation, and one mass was detached. In more lentic habitats and springs, egg masses were most commonly attached to vegetation. A few masses were attached to wood and rocks or detached in lakes. Four masses were in silt in ponds/marshes, and in springs, masses were also attached to wood, rocks, and one mass was found in silt.

Average water depths at egg masses ranged from 0.01 m (sd $=$ 0.03) to 0.19 m (sd $=$ 0.11; Fig. 7, Supplemental Table 1; see Data Accessibility). Eggs were laid at the surface and at depths

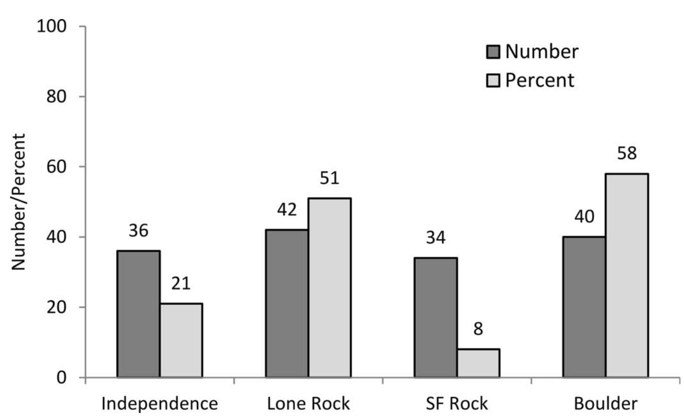

Fig. 4. Number of pools and percent of all habitat types that were pools available to *Rana sierrae* for each survey stream, 2009–2011.

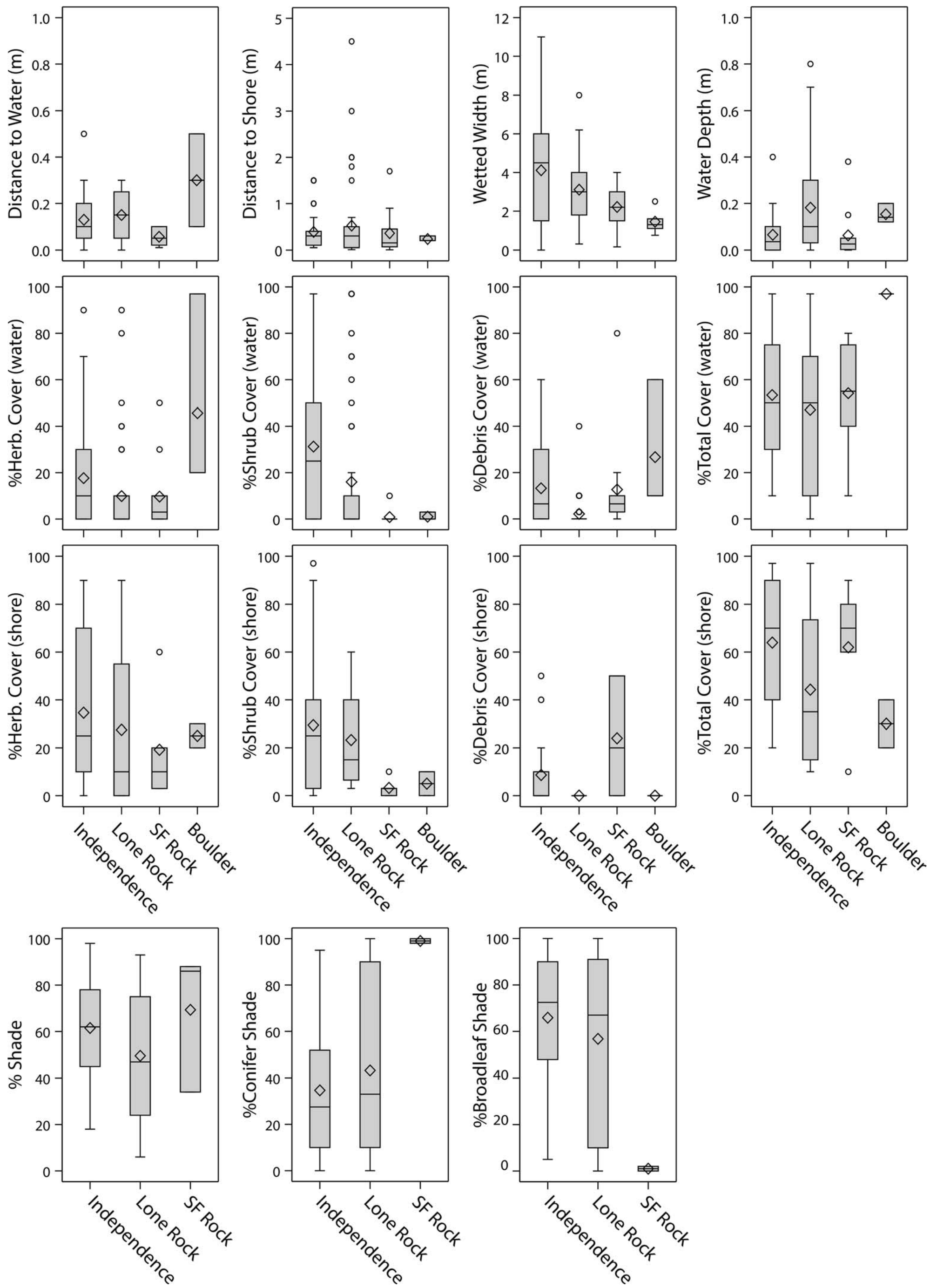

Fig. 5. Location, stream, cover, and shade habitat attributes for locations where marked adult *Rana sierrae* were found for each stream reach, 2009–2011. Diamonds are averages and horizontal lines in center of boxplots are medians. Supplemental Table 3 provides these data in tabular format (see Data Accessibility).

up to 0.47 m, but generally they were not found at the bottom of streams unless they were very shallow. Eggs were typically laid in low flow areas, but flows were low overall in the streams. General egg mass sites tended to be small in width and low to moderate gradient (1–5%). Water depths were deeper at Summit Meadow (average = 0.41 m, sd = 0.09) and Deadwood (average = 0.27 m, sd = 0.12), and most shallow at Ebbetts Pass (average = 0.07 m, sd = 0.05). Egg sites tended to be in more open areas with maximum canopy cover of 32%.

Distance traveled and spatial distribution based on CMR.— Within the four-day CMR periods from 2009–2011, there was a total of 96 recaptures of 45 individual marked frogs (Table 4). On average, frogs traveled 19.9 m (sd = 28.5) between capture locations. The largest distances traveled were by four frogs at Independence Creek in 2010. These frogs moved distances of 77, 117, 155, and 207 m between the June and August surveys. Within each survey period, they tended to stay in the same place and were found in similar locations in each of the August surveys. If these four frogs were excluded, the maximum distance between days was 40 m. Excluding the four frogs, females (average = 16.0 m, se = 1.2) traveled slightly farther than males (average = 11.0 m, se = 2.0). Among years, there were 39 recaptures of 32 individual frogs (Table 5). Frogs moved an average of 69.6 m (sd = 93.7), though the median distance was only 32.8 m. Distances were similar for males and females. The largest observed movement was 481 m, when a female that was found on the upper part of the stream reach at South Fork Rock Creek in 2009 moved upstream to a pond in a meadow in 2010 and 2011.

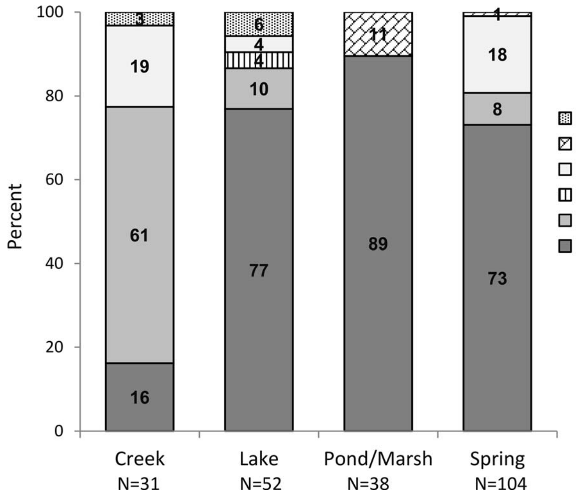

Fig. 6. Egg mass attachment substrates used by *Rana sierrae* by habitat type in five streams in the northern and central Sierra Nevada, surveyed in 2003. Numbers are percents of each habitat type.

At Independence Creek, frogs were found throughout the study stream, but the highest densities were in the middle third of the reach, which corresponds with where we found tadpoles. There was no separation of adults and subadults, though subadults generally were found downstream of breeding areas in 2009 and 2010. At South Fork Rock Creek, adults were found in the same general vicinity at the upper end of the study stream on the stream and in a small pond in the meadow at the top of the reach; only one subadult was found. The lower part of the stream had more dry sections fragmenting the habitat. At Lone Rock Creek, adults were found more often in the upper part of the study stream where the stream was less affected by beaver activity. Subadults and tadpoles were found more often in the lower section that overlapped with the beaver activity and had more flooded grassy areas and backwater refuges. At Boulder Creek, frogs were found in or near small pools in the upper part of the stream reach. Subadults were found in a flooded area created by a beaver dam, and a single tadpole was found just downstream from the beaver dam in a shallow grassy side pool out of the main flow.

Distance traveled and movement patterns based on radio-telemetry.—Twenty-one females and 15 males were radio-tracked at three streams in 2003. The radio-tracked frogs moved up or down the stream reaches relatively frequently over the summer, moving an average of 76% of the tracking sessions. All frogs moved at least once during the summer, and some frogs had moved every survey. Frogs moved an

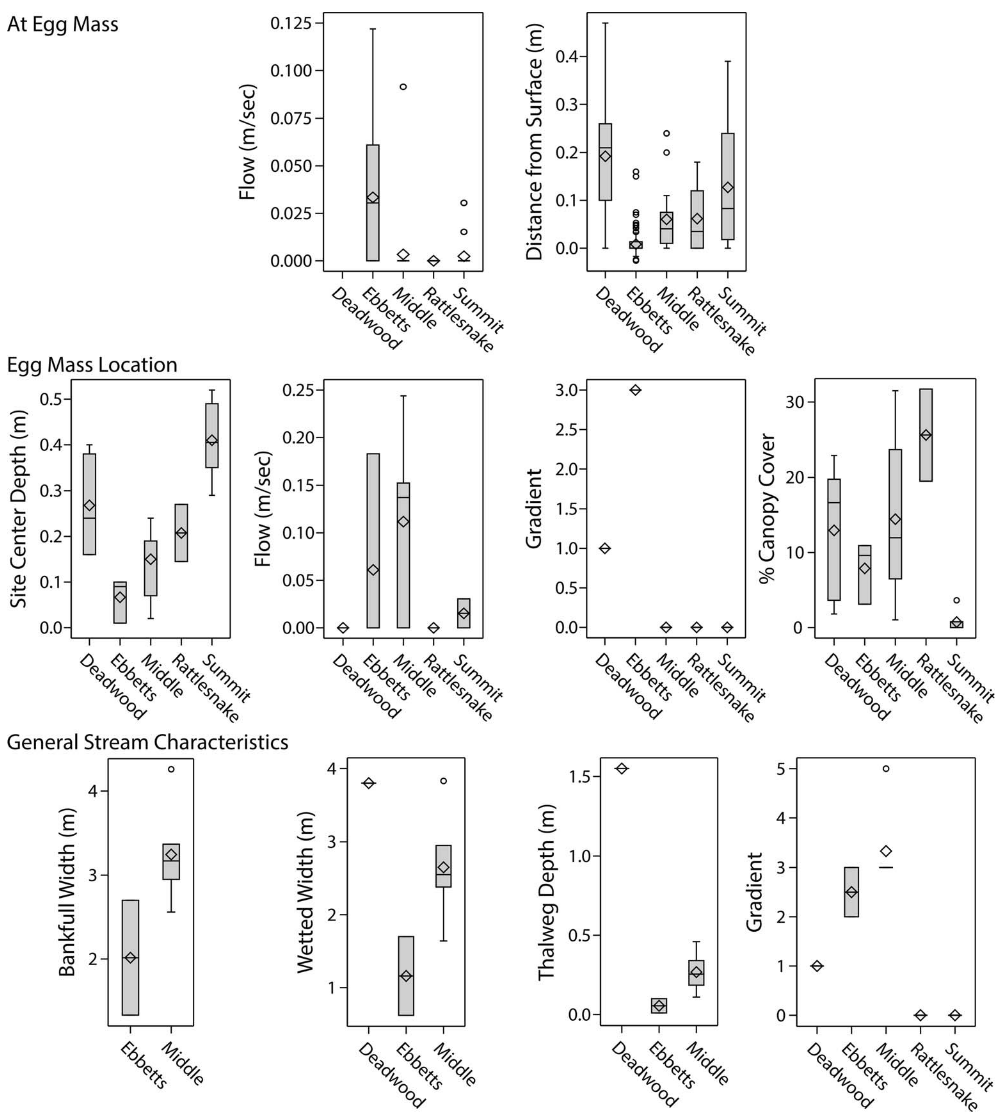

Fig. 7. Microhabitat at egg masses and habitat at egg mass locations in five streams with *Rana sierrae* in the northern and central Sierra Nevada, surveyed in 2003. Diamonds are averages and horizontal lines in middle of boxplot are medians. Supplemental Table 1 provides these data in tabular format (see Data Accessibility).

Table 4. Distances individual PIT-tagged *Rana sierrae* moved between subsequent recaptures within a four day study period, 2009–2011.

	# Individuals	# Recaptures	Distance moved (m)				
			Mean	Median	SD	Min	Max
Overall	45	96	19.9	13.1	28.5	0	207
Females	30	68	18.7	14.5	17.1	0	117
Males	14	25	24.4	10.2	48.4	0	207
Subadult	1	3	10.5	8.6	6.7	5	18

average of 122 m (sd = 103.7) between tracking surveys, with maximum distances averaging 230 m (sd = 182). Total movements over the summer averaged 328 m (sd = 257). Frogs were capable of moving relatively large distances, with 24 of the 36 tracked frogs moving >100 m and six moving >400 m between surveys. The maximum distance traveled was 840 m over 23 days by a male frog at Deadwood Creek. This same male moved a total of 1248 m over the summer. Frogs were always found close to water, though at Deadwood Creek, they occasionally moved short distances (<200 m) overland to nearby water.

Males moved a little more often and slightly greater distances than females. Males moved an average of 81.9% (se = 5.8) of the surveys compared with 71.3% (se = 5.9) of the surveys for females. The median distances traveled by frogs between periods were similar among the sexes (females = 88 m, males = 90 m), but maximum and total distances traveled by males were farther than females. Maximum distances traveled between surveys averaged 265.7 m (se = 56.4) for males compared with 204.7 m (se = 33.0) for females, and total distances traveled over the summer averaged 392.6 m (se = 75.2) for males compared with 282.1 m (se = 49.2) for females. The maximum values of these metrics for males were generally more than twice those for females.

Baker Creek frogs moved the least often and smaller distances than frogs on the other streams, Cow Creek frogs moved the farthest on average, and Deadwood Creek frogs had the longest movements (Fig. 8, Supplemental Table 4; see Data Accessibility). The average percent of surveys that frogs moved was 56.9% (sd = 27.1) for Baker Creek, 70.8% (se = 28.2) for Cow Creek, and 91.7% (se = 21.9) for Deadwood Creek. Median, average, and maximum distances traveled between surveys at Cow Creek were more than twice those at Baker Creek. Finally, more long-distance movements occurred at Deadwood Creek, with four frogs moving >400 m between surveys and two moving >500 m over the summer. No frogs at Baker Creek moved these distances, and at Cow Creek only one frog moved >400 m between surveys and >500 m over the summer. Generally, frogs were found close to shore in open canopy, low gradient locations.

***Chytrid*.**—We collected 234 tissue samples from *R. sierrae* (80 from adults, 122 from subadults, and 32 from tadpoles). Low levels of *Bd* (<400 zoospore equivalents) were detected in only nine frogs. Of the marked individuals, these included a female at Independence Creek that was not infected in 2009 and June of 2010, but had very low levels detected in August of 2010 and 2011, a female at Lone Rock Creek that had *Bd* only the first of the three years it was captured (2009), and a female at Lone Rock Creek that was only captured in 2009. In addition, low levels of infection were detected in an unmarked adult and two subadults at Independence Creek, two subadults at the Beaver Pond meadow, and one subadult at Lone Rock Creek.

DISCUSSION

Populations of *Rana sierrae* generally were small, which corresponds with the species' well-documented population declines (Vredenburg et al., 2007; Brown et al., 2014a). Abundances of all life stages were low, including adults, subadults, and tadpoles. We did find indications of reproduction at all streams where we had population estimates, though no tadpoles were found at South Fork Rock Creek. Only one study stream, Cow Creek in the southern Sierra, had a large number of frogs. Historical and current records for lakes document that populations of *R. sierrae* can be quite large. For example, prior to the arrival of *Bd*, Pope (1999) marked 582 frogs over two years in one study basin, and Vredenburg et al. (2010) reported thousands of frogs (*R. sierrae* and *R. muscosa*) historically occurring in lake-dominated metapopulations throughout Sequoia and Kings Canyon National Parks (also Grinnell and Storer, 1924; Brown et al., 2014a and for *R. muscosa*, Bradford, 1991; Boiano and Meyer, 2010). In contrast, our largest annual stream population based on mark–recapture estimates was two males and 11 females in 2009 and, although less reliable than mark–recapture methods, Deadwood Creek had a count of 34 adults during one survey. Egg mass counts can, in some situations, provide an estimate of numbers of females in a population, and in most of our study streams, the numbers of egg masses also suggest small populations. The apparent discrepancies with number of frogs at some sites could be due to low detectability in adult *R. sierrae* in streams, females laying multiple egg masses, or females moving outside of our study reaches shortly after laying eggs.

To our knowledge, no equivalent historical data exist for stream populations for comparison. In extensive monitoring throughout the Sierra Nevada range of the Mountain Yellow-Legged Frog taxa (2002–2010), frogs of any life stage were

Table 5. Distances individual PIT-tagged *Rana sierrae* moved among years, 2009–2011.

	# Individuals	# Recaptures	Distance moved (m)				
			Mean	Median	SD	Min	Max
Overall	32	39	69.6	32.8	93.7	2	481
Females	22	29	68.4	28.2	100.5	2	481
Males	9	9	76.6	41.1	78.6	2	186
Subadult	1	1	42.2	42.2		42	42

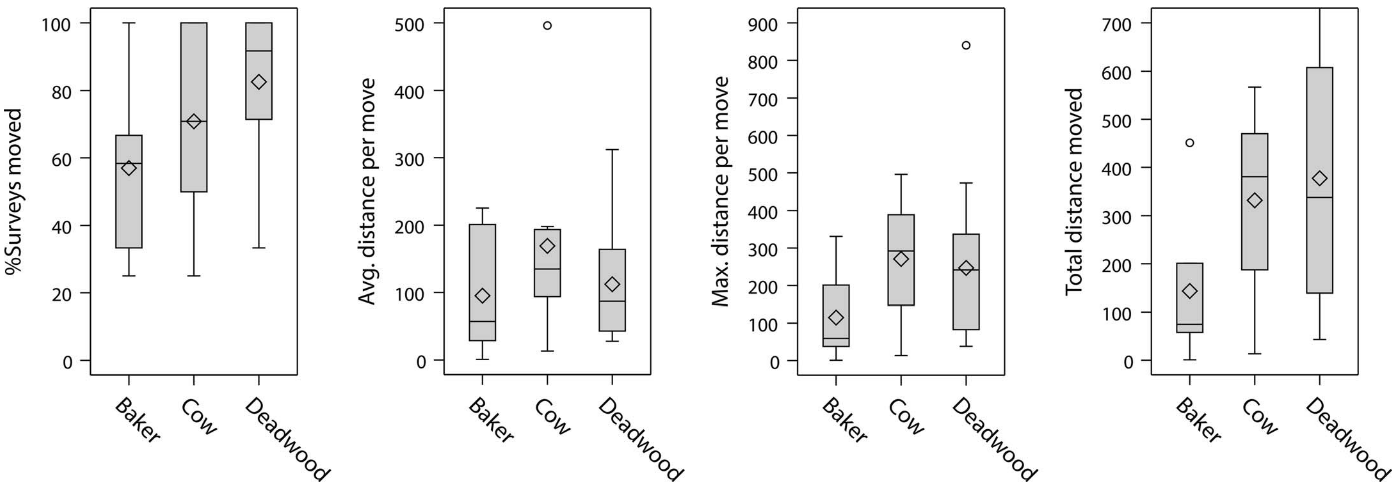

Fig. 8. Frequency and distances radio-tracked *Rana sierrae* moved between subsequent recaptures in 2003. Total distance moved at Deadwood Creek was 1248 m. Diamonds are averages and horizontal lines in middle of boxplot are medians. Supplemental Table 4 provides these data in tabular format (see Data Accessibility).

found in streams in 28 of 51 occupied watersheds, with evidence of reproduction (eggs, tadpoles) in 11. In most of the sample reaches, relative abundances of adults and subadults were low (<10 frogs, maximum = 21). In the two streams with relatively large numbers of tadpoles (1977, 211) only a few adults and subadults were found (Brown et al., unpubl. data). One of these was Rattlesnake Creek, where <10 frogs and 58 tadpoles were found in 2003. Survival rates of *R. sierrae* in our monitoring reaches were relatively high and similar to those found by Matthews and Preisler (2010) in lentic habitats in the southern part of the species' range.

The declines in populations of *R. sierrae* have been largely attributed to the introduction of trout to historically fishless lakes in high elevations and to the spread of *Bd* (Bradford, 1989; Knapp and Matthews, 2000; Vredenburg, 2004; Rachowicz et al., 2006). How these risk factors affect stream populations and their role in explaining the small abundances in our study reaches is not known. Fishes were found in all of the 2009–2011 streams and only in Baker Creek from the 2003 surveys. In the northern streams, fishes were not identified to species; however, they likely included both native and non-native salmonids, and two of the streams are hydrologically connected to reservoirs with fishes. The large population at Cow Creek was not exposed to fishes compared with nearby Baker Creek which had smaller abundances. Few studies provide detailed CMR data on individuals that include disease information (but see Joseph and Knapp, 2018). In this study, we provide these data for multiple populations. *Bd* was found on only four adult and five subadult frogs and at low infection levels in the streams sampled (northern streams). It is unknown whether *Bd* played a role in the current small populations in this region, but it is likely that the disease may have caused declines of these frogs before the *Bd* pathogen was identified (Cheng et al., 2011; Sette et al., 2015). In 2003, *Bd* had not yet invaded Cow Creek, and, after its arrival, this large population was decimated. It has been shown that a combination of high rates of infection and spread, typically found in large populations, can cause populations to collapse (Briggs et al., 2010; Vredenburg et al., 2010). Further, recent research has found that *R. sierrae* can persist with low levels of *Bd* infection (Knapp et al., 2016).

Interestingly, our second largest population was in the meadow associated with beaver activity, where numbers may approach those found currently in some lakes (see Brown et al., 2014a). Tadpoles generally were more common in the deep, open pools, subadults in open, shallower flooded vegetation, and adults in medium-sized pools with more vegetation cover and in the adjacent stream channels. The role beaver play in creating habitat for the predominantly lentic-breeding *R. sierrae* warrants further investigation (Cunningham et al., 2007; James and Lanman, 2012). This is particularly true for places where lentic habitat is scarce, such as the northern range of the species. The few tadpoles we found at Lone Rock Creek and Boulder Creek also appeared to be associated with beaver activity.

The ecology of *R. sierrae* in stream environments is not well known. We found multiple age classes of tadpoles in two of the northern streams confirming that, similar to the rest of the range, they require multiple years to develop at these elevations. Based on knowledge from lake habitats, the multi-year tadpole stage requires breeding habitat that provides a refuge from overwinter freezing (Bradford, 1983; Knapp, 2005; but see Lacan et al., 2008), summer desiccation (Lacan et al., 2008), and fishes (Knapp and Matthews, 2000). During the 2009–2011 surveys, we spent a limited amount of time looking for potential nearby off-channel lentic-breeding areas including deep spring pools, deep potholes, and ponds or lakes. Although we found a few promising locations, we did not find any tadpoles in them. Instead, we found tadpoles in, or adjacent to, the streams. Although the three stream locations were somewhat different (i.e., shallow tributary, streamside bench, small pool), they were all exposed, relatively shallow, and with warm water. These are characteristics typical of tadpole microhabitats in lentic waters (Bradford, 1984; pers. obs.). However, these locations did not have deep water refuges typical of lakes, and how tadpoles overwinter in these habitats is not known.

The ecology of egg mass deposition is also not well known, particularly in streams. Although we cannot determine habitat selection with our data, we generally observed that frogs used a variety of habitats to deposit their eggs based on what was available. *Rana sierrae* laid eggs in inlet creeks, marshy floodplains and ponds adjacent to creeks, and in the creeks themselves. Interestingly, in some locations, *R. sierrae* seemed to prefer creeks even when lake habitats were available. *Rana sierrae* laid eggs near the water surface, mid-column in the water, and near the habitat bottom in shallow areas. Eggs were attached most often to rock substrate in creeks and vegetation in lentic habitats. *Rana sierrae* usually laid their eggs in a highly clustered fashion, though they did not lay their eggs communally. We often observed eggs laid upstream of areas with higher densities of other life stages, though tadpoles from previous years were generally nearby. Egg site selection may be affected by tadpole predation on eggs (Vredenburg, 2000).

The movement ecology of *R. sierrae* in lentic systems has been well studied in one watershed. In this lentic system, adults moved to a variety of other water bodies after breeding and had high site fidelity to these other sites (Matthews and Pope, 1999; Pope and Matthews, 2001; Matthews and Preisler, 2010). Similar patterns have been found for the closely related stream-dwelling *R. boylii* which, in some systems, moves to tributaries during nonbreeding seasons (Bourque, 2008; Gonsolin, 2010). Although our CMR surveys were not designed to address this question and our sample of frogs was small, our data generally corroborate these patterns. Distances between capture sites were small within the four-day CMR periods, and at Independence Creek, several frogs moved longer distances between June and August surveys. Our data also suggest a high degree of site fidelity; 58% of frogs were captured multiple years, distances among years were generally low, and the four frogs that moved large distances from June to August were found in the same areas each August. On the other hand, our radio-tracking data showed that *R. sierrae* regularly moved relatively large distances over longer periods with average distances >100 m between tracking periods, and one frog moved 840 m over a 23-day period. Since our tracking period did not include the breeding period, we were not able to investigate seasonal patterns. Males tended to move more often and greater distances than females. Further telemetry studies examining seasonal movements and investigating how frogs use the available habitat surrounding our study reaches could be illuminating given the differences among reaches in habitat and the surrounding landscape.

The present study demonstrates that *R. sierrae* will use a variety of stream types, including some that are not necessarily what might be expected of such a highly aquatic lake species. Streams were low order, perennial and intermittent, low to high gradient, in meadows and forest, and with a diversity of pool, run, and riffle habitats. In areas that had both stream and pond habitat such as Deadwood Creek, frogs were found predominantly in the stream.

Similar to other studies, we found most of the frogs (67%) in the streams and when on shore, within 1 m of water; we did not, however, search extensively away from water (Zweifel, 1955; Mullally and Cunningham, 1956). We also found frogs basking on shore or in backwaters, tributaries, or side channels. Frogs generally seemed to be selecting pool habitats, with the exception of Lone Rock Creek, which was increasingly affected by beaver activity. At Lone Rock Creek, tadpoles and subadults were found more often adjacent to the deep runs and pools behind beaver dams, whereas adults were found more often in the riffles upstream. Similar to Yarnell et al. (2019, in this volume), we generally found frogs in shallow water, and those authors suggested frogs find similar microhabitats within what may appear to be diverse habitats at larger scales. However, we caution against using simple habitat suitability cutoffs to make specific management decisions given the extensive breadth of habitats used by the species as seen here. Cover appeared to be important and generally took the form of silt, cobble, or boulder substrate. Boulder and rock substrates also provide basking sites. In lakes, Knapp et al. (2003) found a positive association with the percent of silt in the littoral zone among other variables not directly comparable with the present study. Matthews and Pope (1999) found that frogs in August selected for undercut banks and willows, and against bedrock habitats. Overall, *R. sierrae* appears to meet its life history requirements with a wide variety of habitats at multiple scales.

In conclusion, we found both similarities and differences in the ecology of *R. sierrae* in streams compared with lake habitats with implications for the species' conservation. First, the basic life history of *R. sierrae* appeared to be similar in streams and lakes; frogs were always found in or near water, and they appeared to have a multi-year tadpole stage indicating that perennial water is required for successful recruitment. *Rana sierrae* in streams appear to be capable of moving relatively long distances, similar to those in lake environments. Second, the CMR data indicated that northern populations are small, and thus merit recovery actions. The Cow Creek population indicated that stream populations can reach population levels typical of lakes, but whether this was historically common is not known. Egg mass counts were conducted on streams slightly south of the CMR streams and suggested these populations may be slightly larger; still, the egg mass counts indicated small populations relative to historical lake abundances. Causes for the small populations are not known but *Bd* and fishes may have played a role. Finally, the small headwater streams used by *R. sierrae* indicate we should broaden our definition of suitable habitat for the species. Use of perennial streams may be expected for a highly aquatic lake species, but *R. sierrae* also used small intermittent streams with large sections that dried. And, the few breeding sites were not the large deep pools that may have been expected based on a lake paradigm. Further research is needed to determine how the species persists in these habitats. By extending our knowledge on the demography, habitat use, and movements of this federally endangered species in streams, this study adds to the quantitative foundation for developing conservation measures in these under-appreciated habitats. Studies such as ours are critical to provide quantitative baseline information that describes a species niche and the biological constraints imposed on a species (Dodd and Seigel, 1991) given the growing call for incorporating evidence-based science in conservation and management (Cooke et al., 2017).

DATA ACCESSIBILTY

Supplemental information is available at https://www.copeiajournal.org/ce-19-196.

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