

A Lentic Breeder in Lotic Waters: Sierra Nevada Yellow-Legged Frog (*Rana sierrae*) Habitat Suitability in Northern Sierra Nevada Streams

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Ecology of the Sierra Nevada Yellow-Legged Frog (*Rana sierrae*) is well understood in high elevation lakes, but data on habitat preferences in stream-dwelling populations are lacking. We sought to expand understanding of stream habitat use by *R. sierrae* by investigating habitat suitability at the microhabitat and reach scales. We collected habitat availability and use data during 2016–2017 at five stream sites representative of geomorphic diversity in the northern Sierra Nevada mountains of California. At each frog use and availability location, we collected data on geomorphic unit type (e.g., riffles, pools), water depth, water velocity, substrate (e.g., gravel, cobble), and percent cover, including herbaceous, canopy, and total cover. Bootstrapped logistic regression models for all study sites combined indicated water depth and velocity were the strongest predictors of post-metamorphic (adult and subadult) use by *R. sierrae*, while substrate and total cover provided moderate improvement in microhabitat use predictions. Specifically, adults had the highest probability of use in microhabitats with <0.3 m depth and <0.1 m s⁻¹ velocity. For tadpoles, we found velocity was the strongest microhabitat predictor for all study sites combined, with the highest probability of use in habitats with <0.01 m s⁻¹. Site-level models highlighted the relative importance of non-hydraulic habitat variables, such as cover, when suitable depth and velocity conditions occurred. At the reach scale, we found hydraulic conditions varied widely in geomorphic units over time, but suitable microhabitat conditions emerged in differing geomorphic units as flows changed over the season. These data indicate that *R. sierrae*, like other ranid species, may be limited by hydraulically suitable habitat availability, but habitat preferences can be met in a variety of stream reaches when variations in flow conditions over time and space are considered.

ONCE the most abundant frog throughout the Sierra Nevada mountains in California (Grinnell and Storer, 1924), populations of the Sierra Nevada Yellow-Legged Frog (*Rana sierrae*) have been greatly reduced primarily due to impacts from amphibian chytrid fungus (*Batrachochytrium dendrobatidis*; Fellers et al., 2001; Vredenburg et al., 2010) and historical fish stocking practices that introduced trout into naturally fishless habitats (Knapp and Matthews, 2000). As a result, the species was federally listed as “endangered” under the Endangered Species Act (USFWS, 2014), and efforts are underway to recover the species throughout its historical range. Mitochondrial genetic analyses of *R. sierrae* indicated that the species is divided into three distinct groups (“clades”), two of which extend into the northern half of the range (Vredenburg et al., 2007). While many of the remaining populations in the central Sierra Nevada are associated with fishless lentic bodies of water and nearby aquatic habitats (Knapp and Matthews, 2000; Vredenburg et al., 2010), populations of *R. sierrae* in the northern range commonly occur in lotic stream habitat. Yet, knowledge of the ecology and habitat preferences of these stream-dwelling populations is lacking, limiting the ability of resource managers to identify habitat conservation, restoration, and reintroduction options.

The existing literature on ecology and habitat preferences of *R. sierrae* has largely focused on high elevation lakes and associated aquatic habitats in the central Sierra Nevada with little published information on stream habitat use or preferences. In lentic-dominated systems, adults move to different water bodies for breeding and non-breeding

purposes and hold high site fidelity to these locations (Pope and Matthews, 2001; Matthews and Preisler, 2010). Breeding habitats have been found to range from low gradient areas with open canopy and rocky substrates in high alpine lakes to marshy, vegetated lentic areas in the species’ northern range (Brown et al., 2019, in this volume). Adult habitat use in August and early September reflects food demands, while late September and October habitat use reflects refugia demands for overwintering (Matthews and Pope, 1999). Individuals have been observed in areas composed of connected lakes, streams, and meadows where a variety of aquatic habitats are available across breeding, foraging, and overwintering seasons (Pope and Matthews, 2001; Matthews and Preisler, 2010; Fellers et al., 2013). However, as lakes are less ubiquitous in the northern portion of the range of *R. sierrae* and some of the extant populations reside solely in lotic systems (Brown et al., 2019, in this volume), questions remain regarding how *R. sierrae* successfully uses flowing waters within its life history strategy.

Early accounts of habitat use in streams by *R. sierrae* were generally descriptive in nature. For example, Zweifel (1955) described how adult *R. sierrae* could be found along streams with steep gradients and large boulders, as well as low gradient sections with vegetated, silty banks. Mullally and Cunningham (1956) found that a variety of shoreline refugia and basking sites were suitable (e.g., vegetation, wood, undercut banks, debris), but rocks and boulders seemed to be preferred. More recently, state and federal resource agency monitoring studies in the northern Sierra Nevada found adult *R. sierrae* used stream habitats with low canopy cover

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and low flow rates, and were found frequently in pools, but also in riffles in higher gradient stream locations, and in larger numbers near lentic waters associated with beaver dams (Brown et al., 2019, in this volume). Sennett (2017) found the increased sinuosity and presence of riffle and pool habitats in wet meadow streams may benefit adult *R. sierrae* by providing increased food availability and a variety of refugia across seasons. Together these studies suggest that *R. sierrae* occupy a variety of stream habitats, but more quantitative study is needed regarding how different life stages are supported in lotic systems where hydraulic conditions vary seasonally.

We hypothesized that *R. sierrae* may be similar to their sister species, *R. boylei*, which reside solely in mid-elevation streams in California and southern Oregon, in using a variety of stream habitats across their life history as hydraulic conditions change through space and time. *Rana boylei* require specific habitat conditions and productive benthos for successful oviposition and tadpole rearing (Kupferberg, 1996; Yarnell, 2013). Using hydrologic and temperature cues from receding spring flows, adults select low velocity microhabitats for breeding that transition to suitable shallow, low velocity habitats in summer for tadpole rearing (Bondi et al., 2013; Yarnell et al., 2016). In fall, post-metamorphic adults seek overwintering refugia in wet riparian areas to avoid high stream flows over the winter and into the early spring (Bourque, 2008; Gonsolin, 2010). As a result, *R. boylei* select stream reaches with high geomorphic complexity that provide habitats suitable to each life stage with multiple functions (e.g., cover, forage, basking, and breeding) and a greater variety of refugia as flows fluctuate throughout the season (Yarnell, 2008). Interestingly, in a few northern Sierra Nevada streams, *R. boylei* have been found to occupy lower elevation reaches, while *R. sierrae* occupy the higher elevation headwater reaches of the same stream (Bedwell, 2018). Thus, similar to *R. boylei*, populations of *R. sierrae* in these lotic-dominated systems may be successfully using the inherently diverse array of stream flow conditions across intra-annual wet and dry seasons to find suitable habitats for each life stage.

In this study, we explored the use of stream habitats by lotic populations of *R. sierrae* across the breeding and rearing seasons in several geomorphically different streams in the northern Sierra Nevada mountains of California. Specifically, we assessed stream habitat preferences of post-metamorphic frogs and tadpoles of *R. sierrae* at the microhabitat ($\sim 1 \text{ m}^2$) and reach ($\sim 10\text{--}50 \text{ m}^2$) scales and developed stream habitat suitability relationships at the microhabitat scale. These data will help fill gaps in knowledge about stream habitat use by *R. sierrae* as well as provide habitat suitability relationships for use in future habitat-based or individual-based modeling efforts.

MATERIALS AND METHODS

Study sites

Study sites were located on five stream reaches in three watersheds in the northern portion of the range of *R. sierrae* in California with persistent lotic populations (Fig. 1). We selected sites to represent a diversity of watershed area and stream geomorphology in the northern Sierra Nevada; thus, two study sites were located in drainages greater than 25 km^2 , while three were in adjacent connected drainages of less than 5 km^2 (Table 1). Elevation among the study sites ranged from

1455–1955 m, with three study sites located between 1485–1630 m. Each study site had channel morphology typical of northern Sierran streams, with channel gradients ranging from 1.7–11.1%, bed substrates dominated by cobble and boulders, and repeating riffle-pool-run or cascade-pool habitat sequences. The hydrology of each study site also varied with the larger drainages supporting perennial flows, while streams in the smaller drainages were intermittent (Fig. 2). Winter flows were typically an order of magnitude greater than summer low flows at all study sites. Study sites were 425 m to 3 km in stream length and were located within known population areas of *R. sierrae*.

Lone Rock Creek.—Located just west of the Antelope Lake reservoir within the Plumas National Forest, the Lone Rock Creek (LRC) study site was approximately 3 km in length upstream of the confluence with the lake. A perennial stream, LRC was subject to frequent disturbance from high runoff flows. The coarse bed substrate contained a high proportion of fine material that was easily mobilized during high flows. Beaver dams occurred along the stream in several locations creating a series of long deep pools and runs, while high gradient cascades and riffles occurred in more confined channel locations. Both the lake and the stream supported trout (*Oncorhynchus* spp.) and Sacramento Suckers (*Catostomus occidentalis*), yet a small population of *R. sierrae* persisted in the main creek channel upstream of the lake.

South Fork Rock Creek and tributaries.—Within the Plumas National Forest near Deanes Valley, the three South Fork Rock Creek study sites consisted of the mainstem (SFRC) and two associated tributaries, henceforth referred to as South Fork Tributary (SFT) and South Fork Tadpole Tributary (SFTT). The SFRC mainstem study site was approximately 1.2 km long and was located in the upper portion of the watershed approximately 3 km upstream of the SFT tributary junction. The SFT study site was approximately 965 m long and extended upstream from the junction with SFRC to approximately 390 m past the junction with SFTT. The SFTT study site was approximately 425 m long and extended upstream from its junction with SFT. The channel morphology at each study site was dominated by higher gradient cascades and pools with bedrock and boulder substrates. SFRC had a deeper channel valley than the tributaries and the largest proportion of cascade habitat among the three study sites. SFTT had the lowest gradient of each site and a higher proportion of high gradient riffles. Each study site had highly variable flows with high spring runoff becoming intermittent by late summer with isolated pools persisting into late October. A small number of Rainbow Trout (*Oncorhynchus mykiss*) were occasionally observed in the mainstem SFRC and downstream portion of the SFT site.

Independence Creek.—The Independence Creek (IND) study site was located downstream of Independence Lake in the Tahoe National Forest. Unlike the other study sites, the IND study site was located in a multi-channel anabranching reach comprised of a single main channel and several side channels. The mainstem channel was approximately 675 m long, but total stream length including side channels was approximately three times that length. The channel morphology was dominated by lower gradient pools and riffles with coarse substrates in the main channel and finer materials in the side channels. Unlike the other study sites, the perennial stream flows were controlled by managed

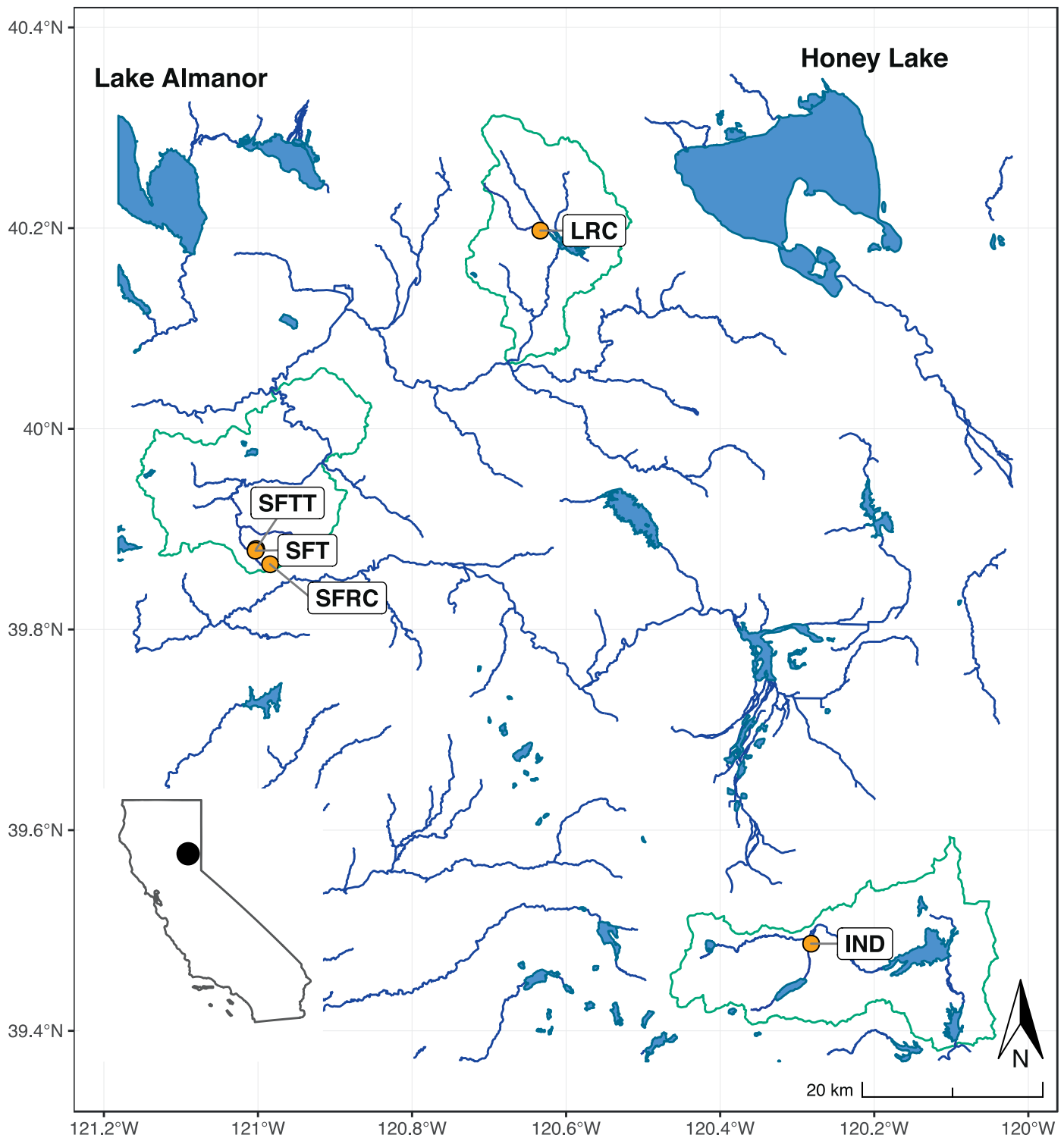


Fig. 1. Study site locations in the northern portion of the range of *R. sierrae*. One study site is located on each of Lone Rock Creek (LRC) and Independence Creek (IND), one study site is located on the mainstem South Fork Rock Creek (SFRC), and two study sites are located on tributaries to SFRC (SFT [South Fork Tributary] and SFTT [South Fork Tadpole Tributary]).

Table 1. Watershed and habitat characteristics of each study site.

	Drainage area (km ²)	Elevation (m)	Site length (m)	Channel slope (m/m)	Dominant morphology	Dominant substrate
Independence Creek	38.9	1955	1870	0.029	pools, riffles	cobble, silt
Lone Rock Creek	29.5	1595	3010	0.017	pools, runs	cobble, silt
SF Rock Creek	4.5	1630	1175	0.081	cascades, pools	boulders, bedrock
South Fork Tributary	3.3	1455	965	0.111	cascades, pools	boulders, bedrock
South Fork Tad Tributary	0.4	1485	425	0.077	cascades, riffles	boulders, bedrock

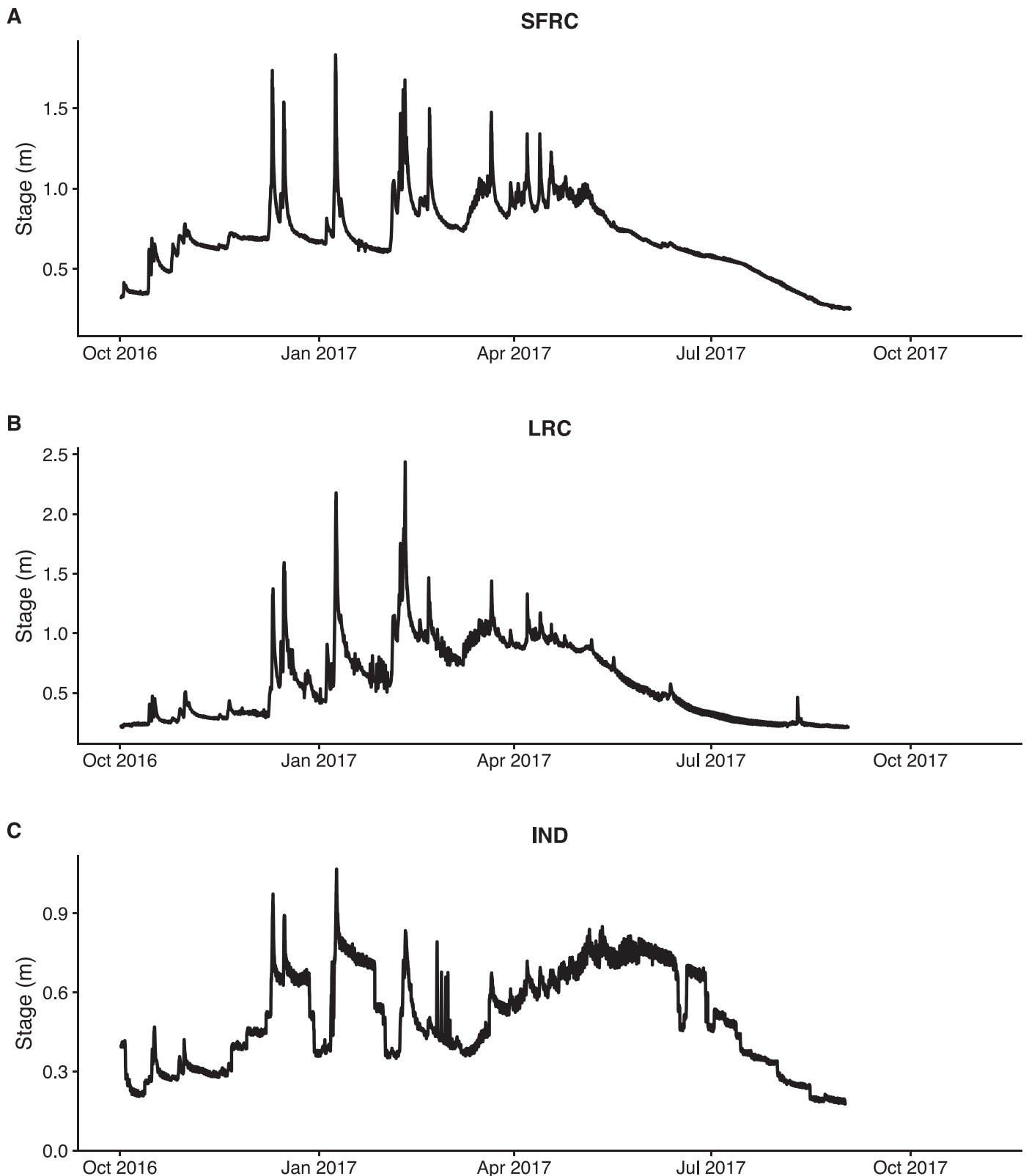


Fig. 2. Hydrographs of stream stage (depth) at three of five study sites in the northern Sierra Nevada over the course of the study. (A) South Fork Rock Creek (SFRC) and (B) Lone Rock Creek (LRC) hydrographs show a strong seasonal signal of winter storm events and spring snowmelt recession into low flow in summer, while (C) Independence Creek (IND) shows modified flow releases in spring and augmented flow releases in late summer from the upstream reservoir. Data were collected with pressure transducers placed in pools that remained wet over the summer.

releases from Independence Lake. While the annual flow pattern generally mimicked the natural seasonal hydrology observed in the unregulated study sites, with higher flows in winter and spring and low flows in summer, abrupt regulated

flow changes were observed in spring (e.g., June 2017) and aseasonal flow releases occurred in late summer and early fall each year (Fig. 2). During high flows in both years, water overtopped the main channel creating shallow floodplain

habitat connected to inundated side channels. During low summer flows, some side channels remained wet from hillslope seepage or overflow from the main channel, while some side channels went dry. A small number of trout (*Oncorhynchus* spp.) and sculpin (Cottidae) were occasionally observed in the main channel.

Habitat use

We conducted visual encounter surveys for tadpoles and post-metamorphic frogs (adults and subadults, hereafter termed just 'adults') monthly in the spring, summer, and fall of 2016 and 2017 and collected data on microhabitat conditions at each observed use location. Each year, we conducted surveys from approximately June through September, for a total of eight surveys at each study site across the study period. During each survey, two surveyors walked or waded along each side of the stream visually searching for any lifestage (Fellers and Freel, 1995). At each observation, either directly adjacent to the individual or in the water immediately proximal to the individual if basking, we measured water depth with a wading rod and mid-column velocity using a Marsh-McBirney Flow Meter (Hach Company, Loveland, CO). Depths <4 cm and occasionally depths between 4–6 cm were too shallow to obtain an accurate velocity if water was visibly flowing; however, if there was no visible flow, these shallow locations were assigned a velocity of 0 m s⁻¹. Dominant substrate for tadpoles and adults was recorded at the observation location and as a categorical variable based on grain size diameter of the median axis: silt/fines, sand (<2 mm), fine gravel (2–16 mm), coarse gravel (16–64 mm), cobble (64–256 mm), boulder (>256 mm), and bedrock (Harrelson et al., 1994). Within a 1 m² plot centered on the individual observation, we also estimated potential refuge cover as the decile percent of herbaceous cover and total cover (comprised of anything a small adult or tadpole could hide under, including silt, boulder crevices, vegetation, algae, wood debris, and flotsam), as well as potential shading cover as the quartile percent of canopy cover (vegetative cover greater than 1 m above the water's surface providing shade). When tadpoles occurred in close proximity to one another and experienced the same microhabitat conditions, we took a single measurement for each habitat variable to represent the group; otherwise, all use observations represented individuals. We recorded geographic coordinates for each observation using a handheld GPS unit, which were overlaid on 10 m resolution orthophoto imagery using a Geographic Information System (ArcGIS 10.3, ESRI, Redlands, CA).

Habitat availability

Stream morphologies and their associated channel habitats are driven by a combination of physical processes that operate at varying hierarchical scales (Frissell et al., 1986; Thomson et al., 2001), where the geomorphic unit serves to link geomorphic processes creating channel morphology and biologic responses of aquatic species, including amphibians, to their physical habitat (Yarnell, 2008). At each study site, we surveyed the longitudinal distribution of geomorphic unit types following the basic classification of Hawkins et al. (1993) and established a series of systematic transects to quantify available microhabitat conditions. We oriented transects perpendicular to streamflow and at equal spacing such that at least one transect was placed in each geomorphic

unit type and the number of transects was in proportion to the availability of geomorphic unit types within each study reach. We monumented these transects for use across the two-year duration of the study as a means of documenting the variability in available microhabitat conditions across seasons.

We measured habitat availability with the goal of 5–7 equally spaced points relative to channel width, with a minimum spacing of approximately 0.25 m, along each transect using a random start point to limit selection bias. For example, if wetted width was 5 m, then a 1 m measurement spacing was selected with the first measurement point randomly occurring within the first meter of the water's edge. At each point, we measured total depth, mid-column velocity, dominant substrate, percent herbaceous cover, percent canopy cover, and percent total cover using the same methods described for habitat use locations. Habitat data collection was limited to locations where it was safe to wade (typically depth <1.5 m or velocity <2 m s⁻¹ during high flows in the spring).

Statistical analyses

We used logistic regression modeling to simultaneously evaluate habitat use and availability and to incorporate all microhabitat variables in a single regression equation. The actual probability of use for any given lifestage is extremely small compared to non-use locations available in a stream environment. Thus, we regarded habitat availability points in this dataset as non-use points and evaluated habitat use points to an equal number of random non-use points (Thomas and Taylor, 2006; Bondi et al., 2013).

We conducted logistic regression using the glm package in R (R Core Team, 2018) and an iterative bootstrapping procedure where each single bootstrap consisted of a single model built with an equal number of use samples and randomly selected availability samples. For each bootstrapped model iteration, we included all use samples from either the tadpole or adult datasets and a random sample of available data from each site equal in number to the use samples from that site. We selected random samples from the availability dataset with replacement using a random seed in R. We repeated this bootstrapping process 1,000 times for each lifestage, and we averaged models to assess both mean trends and variability. We calculated model summaries to show the mean model estimate (regression coefficients), standard error, z-value, and P-value for each predictor variable. We combined data from all study sites to maximize statistical power and to determine the microhabitat conditions most selected for *across* study sites regardless of local site heterogeneity. We then *post hoc* explored *within* site microhabitat selection at two study sites with adequate data using the same statistical approach. These were Independence Creek and the combined data from the South Fork tributaries; it was sensible to combine the latter two sites because they were similar in abiotic characteristics and geographically close together (Fig. 1, Table 1).

To further explore how microhabitat use by *R. sierrae* varied given seasonal changes in hydraulic habitat availability, we developed habitat suitability relationships for those predictor variables determined to be most significant from the logistic regression modeling. Habitat suitability relationships and criteria are commonly used to evaluate instream habitat conditions for various aquatic species and lifestages in habitat modeling (Bondi et al., 2013), individual-based

modeling (Railsback et al., 2016), and regulated stream management (Yarnell et al., 2016). Habitat assessment models and individual-based models require discrete quantifications of suitable physical habitat conditions for each lifestage in order to evaluate conditions for successful reproduction or changes in population responses, respectively. For example, Yarnell et al. (2016) used percentile-based habitat suitability indices for defining ranges of suitable hydraulic conditions for amphibian reproduction, while Railsback et al. (2016) used minimum and maximum thresholds of hydraulic and temperature conditions and binary responses for presence of cover or velocity shelters (coarse substrate) for defining suitable amphibian breeding conditions. Following the methods of Bondi et al. (2013), we created categorical habitat suitability relationships for each significant microhabitat variable for each lifestage that reflected the habitat preferences of observed individuals at our study sites. We assigned ranges of observed use to one of two categories. Habitat conditions in which 90% of observed use occurred were quantified as ‘high’ suitability, and conditions of ‘low’ suitability encompassed the remaining 10% of observations. While not transferable to other study sites without adequate testing (Bondi et al., 2013), the relationships developed in this study provided a quantification of observed habitat preferences at our study sites for additional analysis into changing hydraulic conditions across seasons.

To assess potential habitat preferences at the reach scale associated with channel geomorphology, we used a chi-square test to test the null hypothesis that frogs were equally spaced throughout each study site relative to geomorphic unit type (i.e., the number of frogs observed in each geomorphic type was proportional to the relative abundance of each type). We determined the availability of each geomorphic unit type within a study site based on stream length in ArcGIS and statistically compared the percent of available types to the observed percentage of individuals of each lifestage in each geomorphic unit type.

RESULTS

Stream microhabitat use by lifestage

We documented a total of 286 adult and 95 tadpole habitat use observations in monthly surveys conducted during spring and summer of 2016 and 2017 for all study sites combined (Table 2). We collected a total of 4,840 habitat availability point measurements for all surveys and sites combined during the study. Across study sites, both adult and tadpole *R. sierrae* selected a subset of available microhabitat conditions. Adults were found in microhabitats with a mean water depth of 0.14 m (\pm [SD] 0.13) and mean mid-column velocity of 0.03 m s⁻¹ (\pm 0.08) when all study sites were combined (Fig. 3A). The deepest location an adult was observed at any site was at 0.85 m and the highest mid-column velocity was 0.91 m s⁻¹. Boulder and silt were the most frequently used substrates (Fig. 4A), and adults were found in locations with moderate to high percentages of total cover (Fig. 5A). Tadpole rearing sites had very low velocities, averaging 0.01 m s⁻¹ (\pm [SD] 0.01), and an average total depth of 0.19 m (\pm 0.17) when all study sites were combined (Fig. 3B). The deepest location a tadpole was observed at any site was at 1.2 m and the highest mid-column velocity was 0.11 m s⁻¹. The most frequently used dominant substrate was silt (Fig. 4B), and tadpoles were found in locations with higher

Table 2. Summary of number of use and available observations at each study site in each year. IND = Independence Creek, LRC = Lone Rock Creek, SFRC = South Fork Rock Creek, SFT = South Fork Tributary, SFTT = South Fork Tadpole Tributary.

Study site	Year	Available count	Use: tadpoles count	Use: adults count
IND	2016	848	13	35
	2017	1310	43	33
LRC	2016	891	1	24
	2017	835	5	8
SFRC	2016	124	1	12
	2017	270	0	8
SFT	2016	185	1	53
	2017	173	4	41
SFTT	2016	60	11	28
	2017	144	16	44

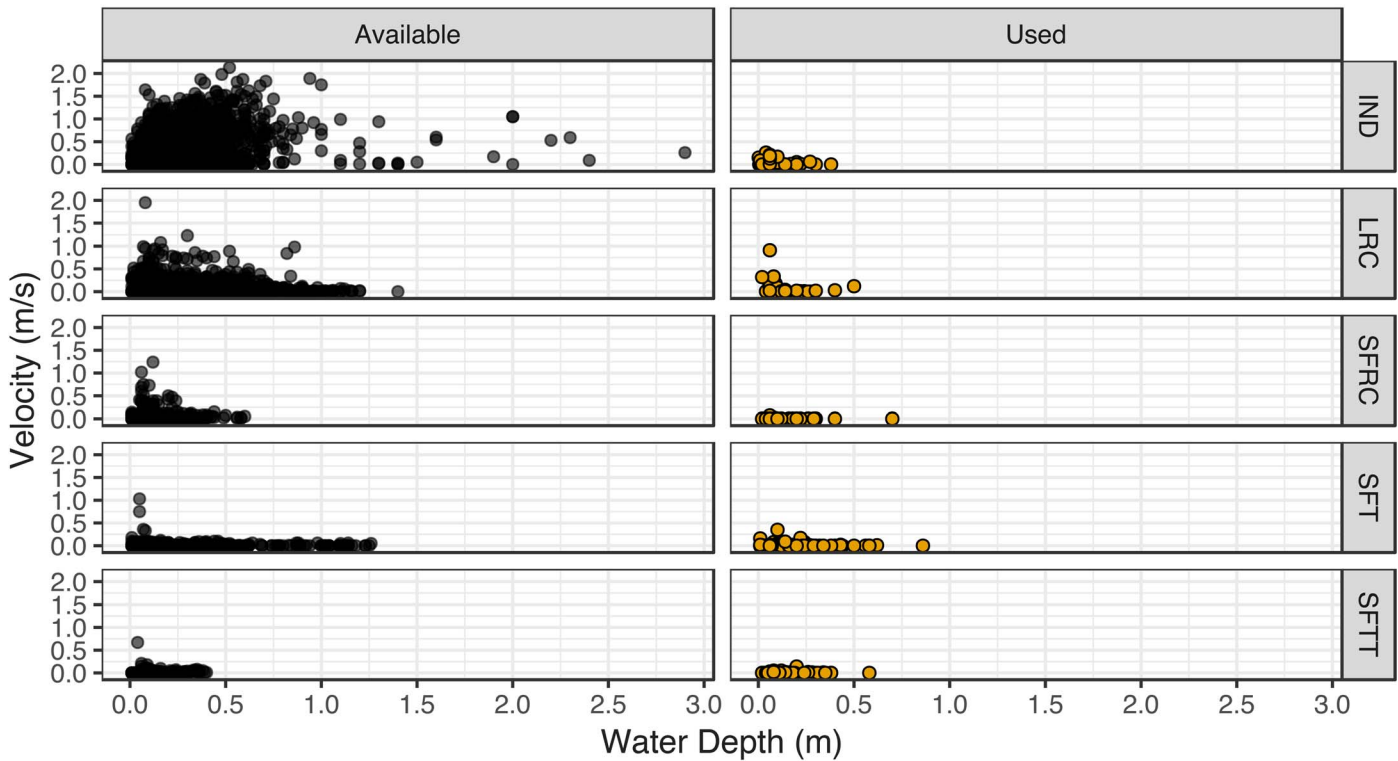
percentages of total cover (Fig. 5B). Because portions of the center of the stream channel were not able to be surveyed during high flows, the habitat availability data predominantly reflected areas that could be surveyed with depths up to 1.25 m and velocities <1.5 m s⁻¹; however, we occasionally collected some availability data beyond these bounds when possible, reflecting the larger range of available hydraulic conditions than was often measurable at higher flows (Fig. 3). Thus, the availability data underestimated the actual amount of deeper water and faster velocities that occurred during higher flows.

Microhabitat preferences

To determine which microhabitat variables were suitable for inclusion in the logistic regression, we completed a non-parametric cross-correlation analysis and excluded the less descriptive variable of any correlated pair of variables (based on Spearman’s Rho values > 0.4). Herbaceous cover was significantly correlated with total cover (Rho = 0.536, P < 0.0001), and canopy cover was significantly correlated with total cover (Rho = 0.457, P < 0.0001). As herbaceous cover was a subset of total cover, and total cover was a better descriptor of the immediate microhabitat conditions surrounding the individual than canopy cover, we chose to retain total cover in the models. As a result, a total of four habitat variables were included in the logistic regression (mid-column velocity, water depth, dominant substrate, and total cover) along with year and month variables to account for temporal and seasonal differences in the data.

Adults.—Logistic regression modeling used an iterative bootstrapping procedure where each single bootstrap consisted of a single model built with all 286 use samples for adults, using a total of 1,000 bootstraps. An equal number of availability (non-use) samples were randomly selected from each site in proportion to the number of use samples from each site. The mean model estimates for adults showed water depth, total cover, and mid-column velocity were the most significant and strongest habitat predictor variables for all study sites combined (Table 3). Substrate moderately improved habitat use predictions. The predicted probability of adult use was highest at low velocities, low to moderate depths, moderate to high total cover, and finer substrates, though probability of substrate use did not vary widely across substrate size (Fig. 6). Month was also a strong predictor variable reflecting the

A Adult RASI



B Tadpole RASI

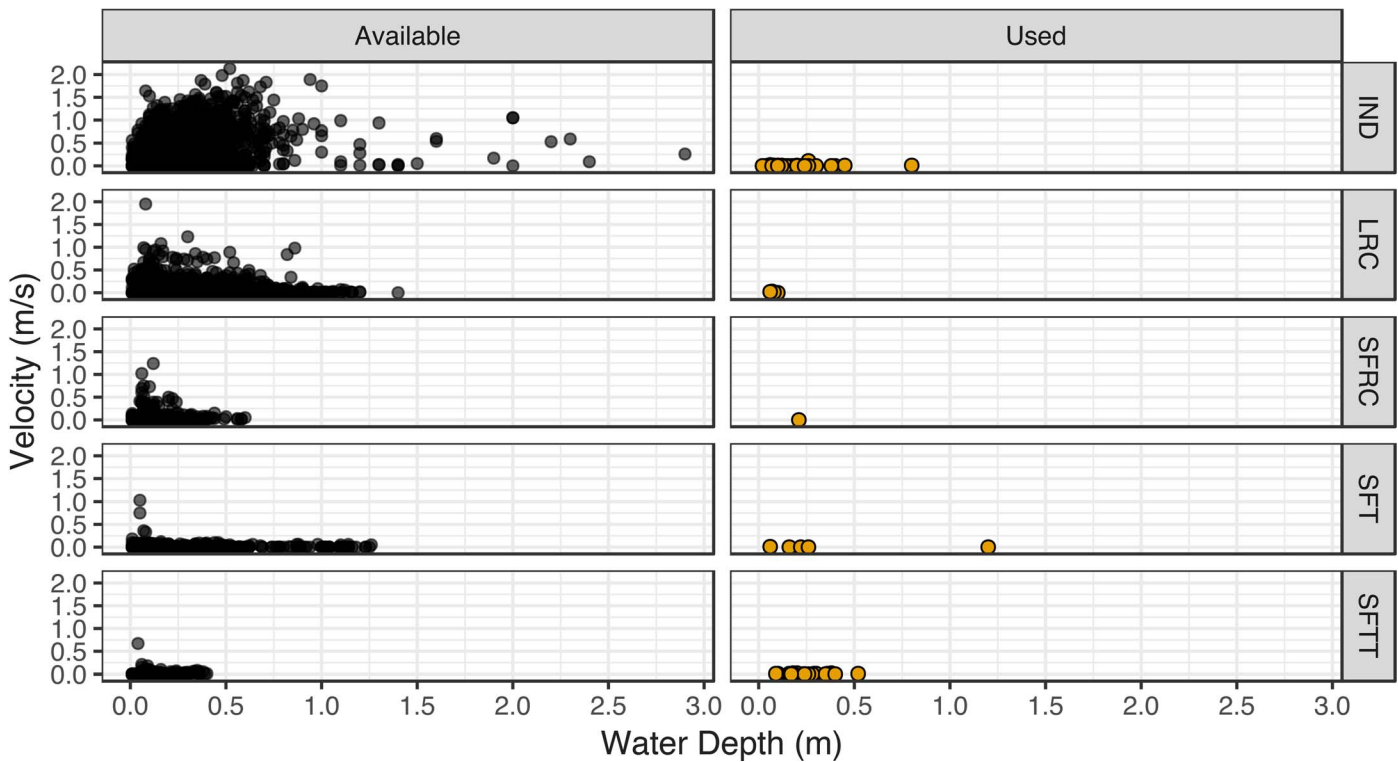


Fig. 3. Hydraulic variables measured for locations and available microhabitat points of (A) adult and (B) tadpoles of *R. sierrae* in five study sites in the Sierra Nevada. Figures show the relationship between total depth and mid-column velocity at both use and available locations for (A) adults (includes subadults) and (B) tadpoles at each study site. IND = Independence Creek, LRC = Lone Rock Creek, SFRC = South Fork Rock Creek, SFT = South Fork Tributary, SFTT = South Fork Tadpole Tributary.

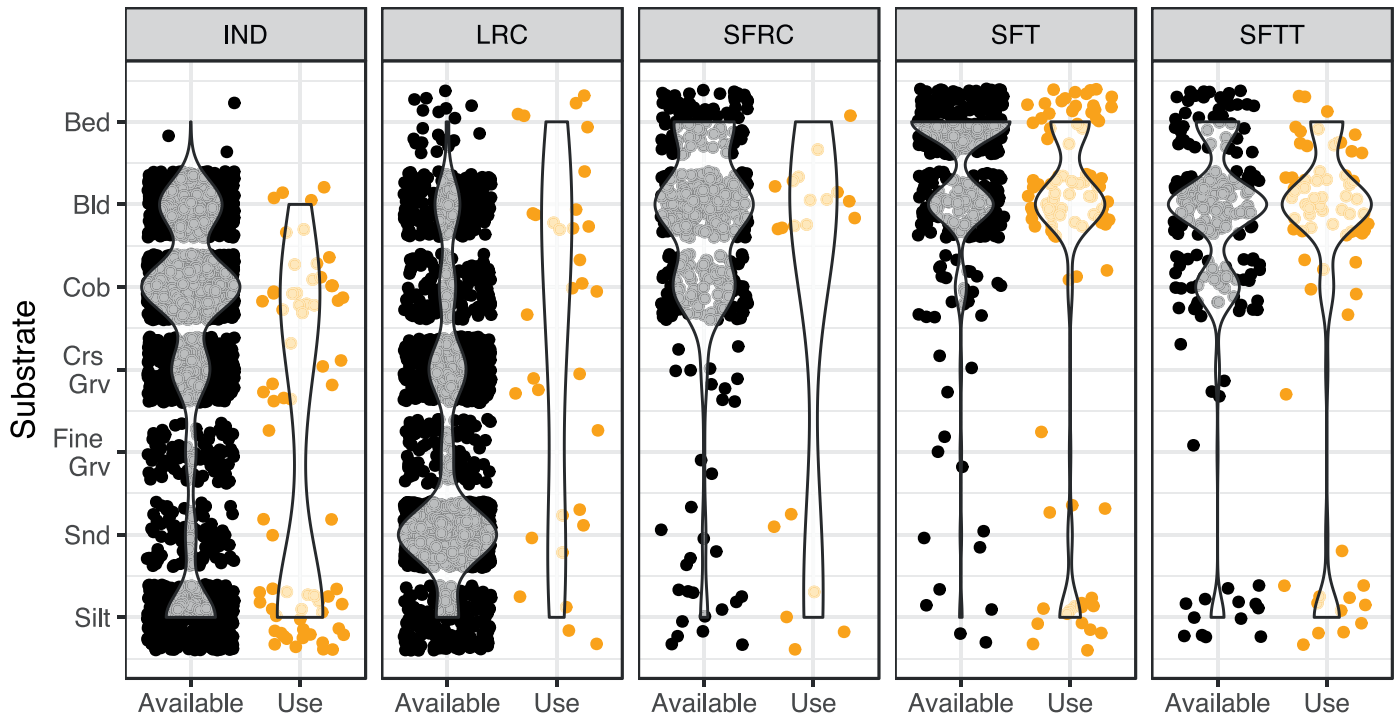
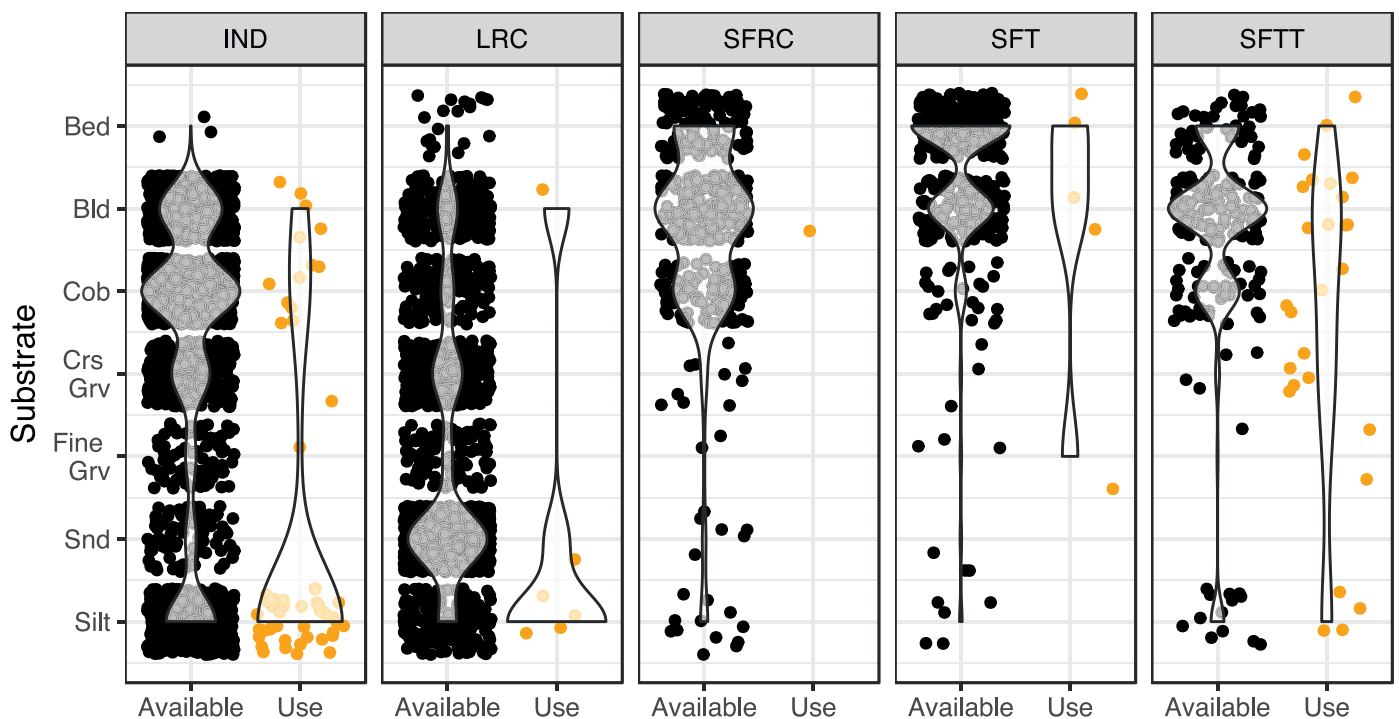
A Adults: Substrate**B** Tadpoles: Substrate

Fig. 4. Distribution of use and available microhabitat points within each substrate category for locations of (A) adult (includes subadults) and (B) tadpoles of *R. sierrae* at each study site. To better visualize the number of points within each substrate category, violin boxplots were overlaid onto jittered points for each substrate category. The overlay shows a mirrored kernel density estimation for all substrate size categories to illustrate the distribution of the data. IND = Independence Creek, LRC = Lone Rock Creek, SFRC = South Fork Rock Creek, SFT = South Fork Tributary, SFTT = South Fork Tadpole Tributary.

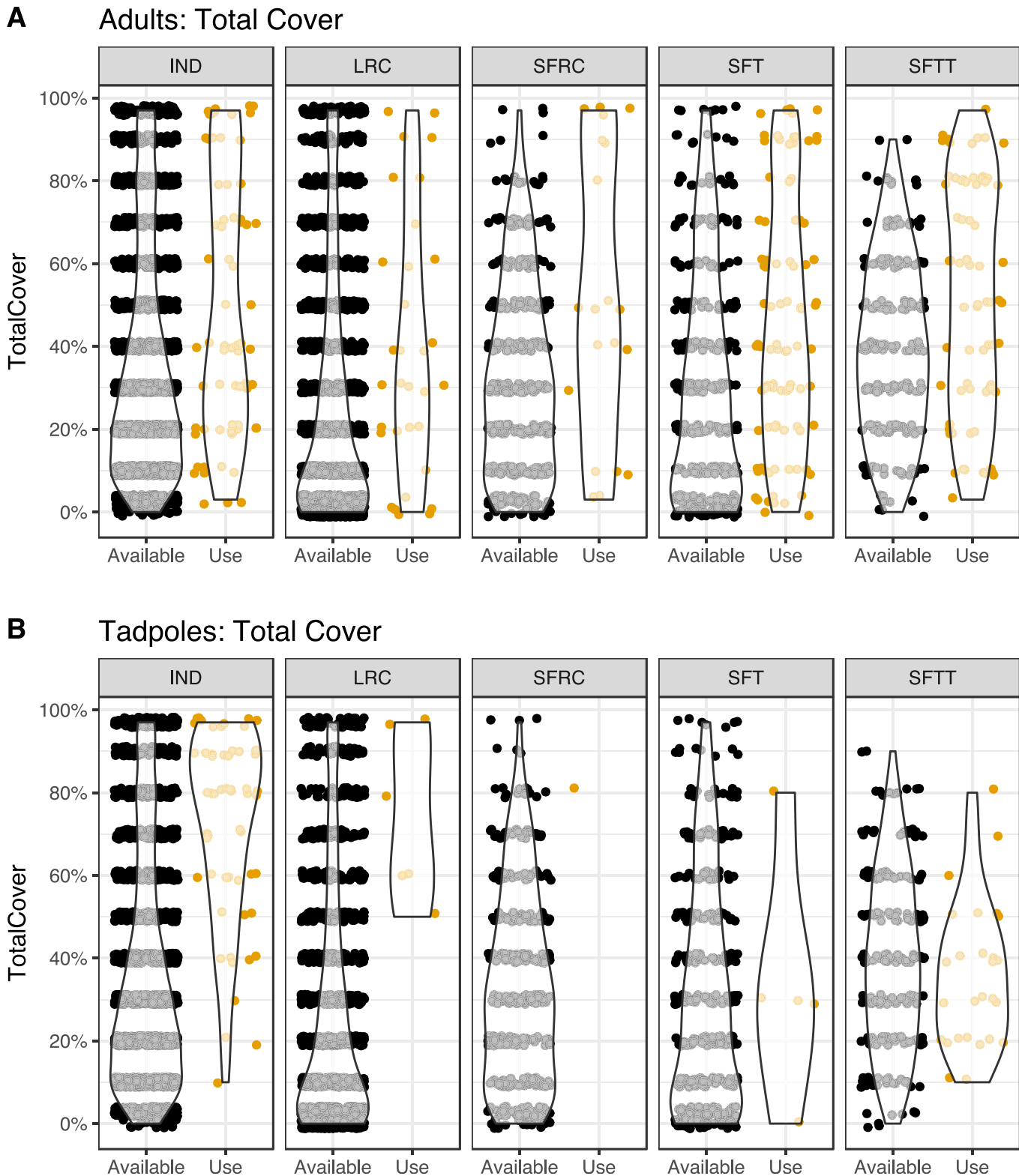


Fig. 5. Distribution of use and available points within each total cover decile for locations and available microhabitat points of (A) adult (includes subadults) and (B) tadpoles of *R. sierrae* at each study site. To better visualize the number of points within each decile, points are jittered. Overlay shows a mirrored kernel density estimate for total cover deciles to illustrate the distribution of the data. IND = Independence Creek, LRC = Lone Rock Creek, SFRC = South Fork Rock Creek, SFT = South Fork Tributary, SFTT = South Fork Tadpole Tributary.

increased likelihood of observing adults as the summer progressed and flows decreased. Year was not a significant predictor for the adult logistic regression models.

To further explore potential variations in adult habitat preferences within study sites, we ran two additional *post hoc*

logistic regression models for Independence Creek and the South Fork tributaries (SFT and SFTT). The mean model estimates for adults at Independence Creek showed similar results to the model for all study sites with water depth and mid-column velocity as the strongest habitat predictors

Table 3. Logistic regression modeling summary for microhabitat use by adult *R. sierrae* for all study sites combined. Model estimates are mean values for 1,000 bootstrap iterations.

	Estimate	Standard error	Z-statistic	P-value
Water depth	-3.867	0.660	-5.854	<<0.0001
(Intercept)	-3.715	0.775	-4.788	<<0.0001
Mid-column velocity	-3.245	0.987	-3.284	0.002
Substrate	-0.104	0.050	-2.064	0.072
Year	-0.194	0.221	-0.879	0.419
Total cover	0.019	0.004	5.032	<<0.0001
Month	0.580	0.088	6.593	<<0.0001

(Table 4). The predicted probability of adult use was highest at low water depths and velocities and slightly higher at finer substrate sizes and larger total cover values (Fig. 7A). Conversely, total cover, water depth, and substrate were the strongest habitat predictors at the South Fork tributaries, while velocity did not significantly distinguish use from availability as all velocities surveyed were low (Table 4). Thus, predicted probability of adult use at the South Fork tributaries was highest in shallow water depths, finer substrates, and greater total cover (Fig. 7B). As with the adult model for all study sites combined, month was a strong predictor in the South Fork tributaries site model reflecting an increased likelihood of observation in later summer.

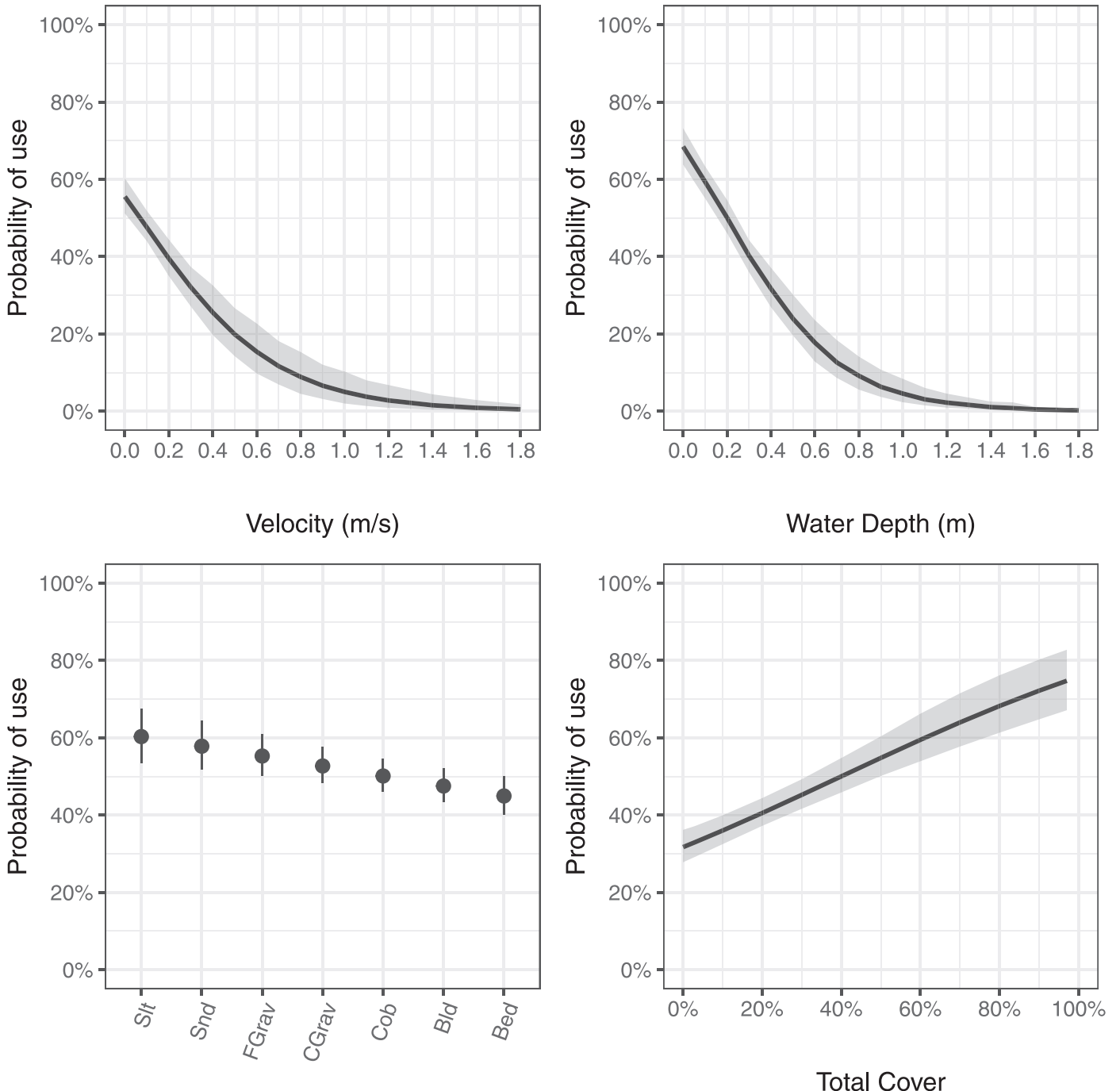


Fig. 6. Mean predicted probability of microhabitat use by adult *R. sierrae* (includes subadults) for all study sites combined for all possible values from a given predictor variable from the 1,000 bootstrapped logistic regression models. Shading and bars represent 95% credible intervals. Substrate categories are silt (Slt), sand (Snd), fine gravel (FGrav), coarse gravel (CGrav), cobble (Cob), boulder (Bld), and bedrock (Bed).

Table 4. Logistic regression modeling summary for microhabitat use by adult *R. sierrae* at Independence Creek (IND) and the South Fork tributaries (SFT & SFTT). Model estimates at each study site are mean values for 1,000 bootstrap iterations.

Site	Variables	Estimate	Standard error	Z-statistic	P-value
IND	Water depth	-12.091	3.035	-3.973	<0.001
	Mid-column velocity	-9.761	3.094	-3.142	0.004
	Year	-0.671	0.666	-0.995	0.362
	Substrate	-0.160	0.172	-0.919	0.400
	(Intercept)	0.752	2.059	0.333	0.504
	Month	0.294	0.240	1.211	0.305
	Total cover	0.014	0.011	1.254	0.296
SFT & SFTT	Water depth	-2.628	0.733	-3.581	0.001
	(Intercept)	-3.741	1.062	-3.520	0.006
	Substrate	-0.205	0.083	-2.449	0.032
	Year	-0.006	0.291	-0.025	0.606
	Mid-column velocity	0.552	2.870	0.011	0.508
	Total cover	0.019	0.005	3.735	0.001
	Month	0.611	0.116	5.264	<<0.0001

Tadpoles.—Similar to the adult habitat models, we completed the logistic regression using an iterative bootstrapping procedure where each single bootstrap consisted of a single model built with all 95 use samples for tadpoles and an equal number of randomly selected availability (non-use) samples from each site in proportion to the number of use samples from each site. The mean estimate values for the tadpole models showed mid-column velocity was the single most significant and strongest predictor variable (Table 5). The predicted probability of tadpole use was highest at very low velocities and positively related to total cover (Fig. 8). Predicted probability of substrate use was approximately even across substrates and water depth, and prediction intervals had high variability. Unlike the adult models, month was not as significant a predictor in the model.

Similar to the adult microhabitat analysis, we ran two additional *post hoc* logistic regression models for tadpoles at Independence Creek and the South Fork tributaries (SFT and SFTT) to explore rearing habitat preferences within study sites. The mean model estimates for tadpoles at Independence Creek showed mid-column velocity was the single significant habitat predictor variable (Table 6). The predicted probability of tadpole use was highest at very low velocities, but did not vary substantially across water depth, substrate size, or total cover values (Fig. 9A). Similarly, mid-column velocity was a strong habitat predictor at the South Fork tributaries, but water depth was a strong habitat predictor as well (Table 6). Thus, predicted probability of tadpole use at the South Fork tributaries was highest in very low velocities and moderately deep water depths (Fig. 7B).

In order to quantify microhabitat use preferences for each life stage across study sites for further analysis of changing hydraulic conditions at our study sites and to compare with other species' habitat preferences, we created a set of habitat suitability relationships for those predictor variables shown to be most significant in the logistic regression modeling and exhibiting thresholds of use. For adults, water depth, total cover, and velocity were the most significant habitat predictors for all study sites combined, with inflection points observed in the predicted habitat use relationships for velocity and water depth. Across our study sites, all adult observations occurred at locations with velocities <0.91 m s⁻¹ and 90% of observations were at velocities <0.09 m s⁻¹ (Fig. 3A). The predicted probability of adult use for all study

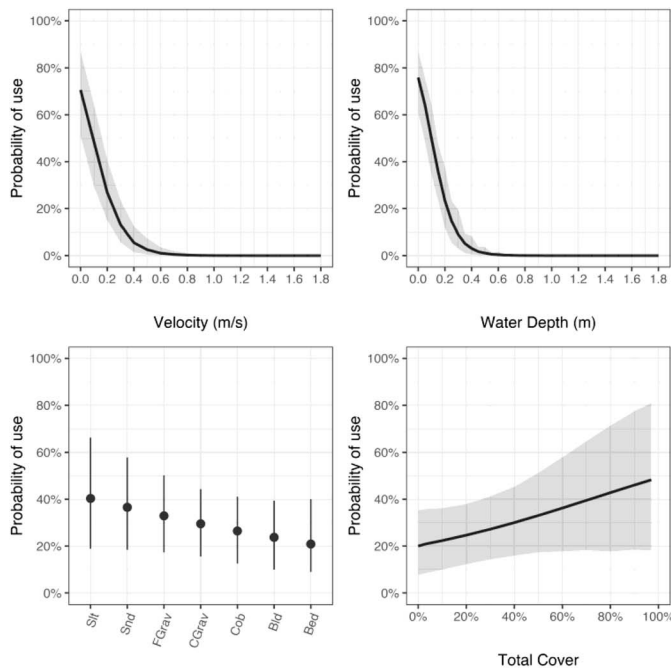
sites combined was highest at velocities <0.1 m s⁻¹ and decreased to less than 10% at 1.0 m s⁻¹, with an inflection point in the curve at approximately 0.7 m s⁻¹ (Fig. 6). Water depths at observed adult locations were also lower than available, with 90% of adult use occurring at depths <0.3 m, and no use observed at depths >0.86 m (Fig. 3A). With a similar pattern to velocity, the predicted probability of adult use was highest at depths <0.2 m and decreased to less than 10% at 0.8 m, with an inflection in the curve at approximately 0.7 m (Fig. 6). Based on the preference for low depth and low velocity microhabitats, we quantified highly suitable microhabitat for adults at our study sites as <0.3 m and <0.1 m s⁻¹, and microhabitat with deeper or faster hydraulic conditions as less suitable (Table 7). While total cover was a significant predictor in the logistic regression model for adults across all study sites, the predicted probability of use did not vary widely across possible values and discrete thresholds or inflections in the curve were not observed (Fig. 6). Thus, we did not quantify categorical habitat suitability relationships for cover for adults.

For tadpoles, mid-column velocity was the most significant habitat predictor for all study sites combined, with a distinct threshold of use at 0.11 m s⁻¹ where no observations occurred at higher velocities (Fig. 3B). Furthermore, 90% of tadpole observations were at velocities of 0.01 m s⁻¹ or less. The predicted probability of tadpole use for all study sites combined reflected these thresholds with the highest modeled probabilities at velocities close to 0.0 m s⁻¹, an inflection point in the curve at 0.1 m s⁻¹, and no predicted tadpole use at velocities >0.2 m s⁻¹ (Fig. 8). Thus, we quantified highly suitable microhabitat for tadpoles at our study sites as <0.01 m s⁻¹, and microhabitat with faster hydraulic conditions as less suitable (Table 7). While total cover, substrate, and water depth were significant predictors in the logistic regression model for tadpoles for all study sites combined, the predicted probabilities of use did not vary widely across possible values and discrete thresholds or inflections in the curve were not observed (Fig. 8). Thus, we did not quantify high or low habitat suitability relationships for these remaining habitat variables.

Reach-scale habitat preferences

The distribution of geomorphic unit types within each study site varied by watershed. The larger perennial streams

A INDEPENDENCE CREEK



B SOUTH FORK TRIBUTARIES

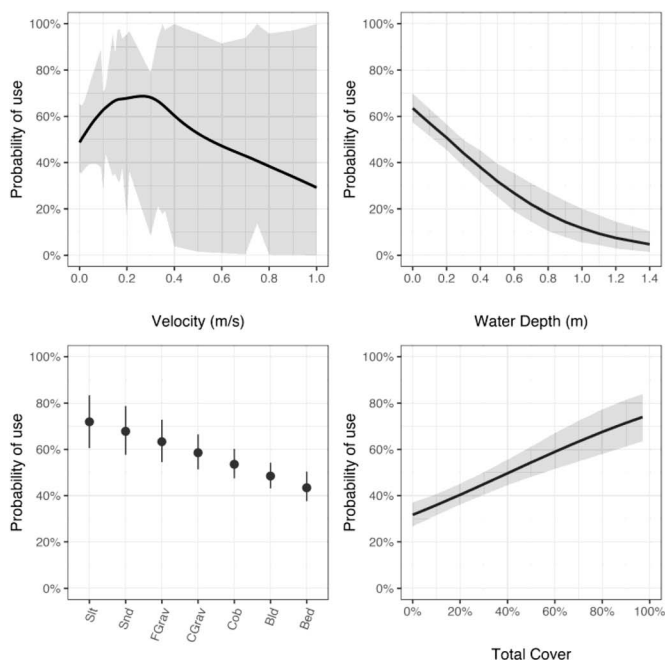


Fig. 7. Mean predicted probability of microhabitat use by adult *R. sierrae* (includes subadults) for all possible values from a given predictor variable from the 1,000 bootstrapped logistic regression models at (A) Independence Creek and (B) South Fork Tributaries. Shading and bars represent 95% credible intervals. Substrate categories are silt (Slt), sand (Snd), fine gravel (FGrav), coarse gravel (CGrav), cobble (Cob), boulder (Bld), and bedrock (Bed).

(Independence Creek and Lone Rock Creek) had reaches with cascades and high gradient riffles, but they were dominated by lower gradient geomorphic units such as runs and pools (Table 8). The smaller intermittent streams (South Fork Rock Creek and South Fork tributaries) were dominated by steeper gradient geomorphic types such as cascades and step-pools.

Table 5. Logistic regression modeling summary for tadpole microhabitat use for all study sites combined. Model estimates are mean values for 1,000 bootstrap iterations.

	Estimate	Standard error	Z-statistic	P-value
Mid-column velocity	-48.751	13.831	-3.517	0.001
Substrate (Intercept)	-0.238	0.105	-2.233	0.072
Water depth	1.552	1.276	1.066	0.346
Year	0.677	0.509	1.324	0.278
Month	0.266	0.185	1.440	0.258
Total cover	0.015	0.008	1.726	0.163

Adult *R. sierrae* were observed in all geomorphic unit types in the larger streams, and almost all geomorphic types in smaller intermittent streams (Table 8), but results from the chi-square tests revealed statistically significant habitat preferences at all study sites except Independence Creek. On South Fork Rock Creek and the South Fork tributaries, adults were found more often than expected in pools and step-pools, and less often than expected in cascades ($P \ll 0.001$, $\chi^2 = 37.3\text{--}46.0$). On Lone Rock Creek, the opposite was true as adults were found more often than expected in cascades and high gradient riffles, but less often than expected in runs and pools ($P \ll 0.001$, $\chi^2 = 42.0$). On Independence Creek, adults were found in all geomorphic unit types in approximately the same proportion as the geomorphic types were available.

Tadpoles of *R. sierrae* were observed in only a few geomorphic unit types at each study site, primarily due to concentration at breeding locations (Fig. 8). However, tadpoles were found more often than expected in pools at all sites except SFTT, where they occurred more often than expected in cascades ($P \ll 0.001$, $\chi^2 = 39.3\text{--}128.4$). Tadpoles were observed occasionally in high and low gradient riffles at Lone Rock Creek and Independence Creek, but in lower proportions than expected based on availability.

To further explore the relationship between geomorphic unit types and the presence of suitable habitat based on the habitat suitability relationships quantified for our study sites, we assessed the change in hydraulic variables, specifically velocity and depth, within geomorphic unit types over time. In particular, we focused on those geomorphic units that were selected more or less often than expected at various sites. Pools typically maintained a range of depths in spring and summer with the highest depths of all geomorphic types across the seasons (Fig. 10). Velocities in pools remained low in both late spring and summer, serving to provide suitable hydraulic habitat for both adults and tadpoles across the breeding and rearing season. Cascades, on the other hand, had high velocities and moderate depths in late spring, but transitioned to low velocities and lower depths as flows decreased and pockets of slow water remained between larger boulders (Fig. 10). As hydraulic conditions changed in cascades, increasing amounts of suitable habitat for adults and tadpoles occurred into summer. Low and high gradient riffles generally provided higher velocities and lower depths across the spring and summer seasons. While generally less suitable due to higher average velocities, riffles by summer provided shallow depths and moderately low velocities that were within the range of suitable values for adults.

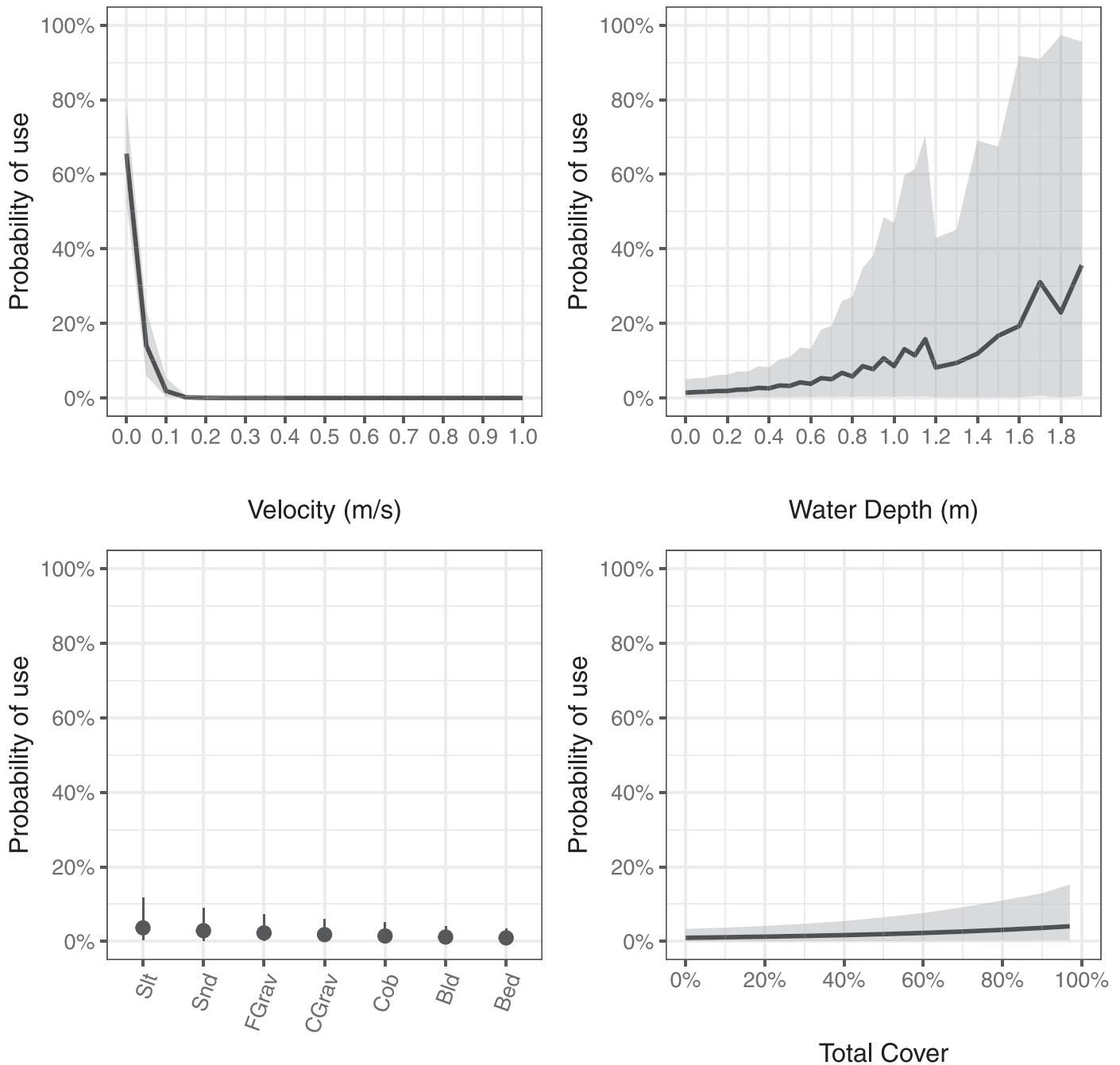


Fig. 8. Mean predicted probability of microhabitat use by tadpoles of *R. sierrae* for all study sites combined for all possible values from a given predictor variable from 1,000 bootstrapped logistic regression models. Shading and bars represent 95% credible intervals. Substrate categories are silt (Slt), sand (Snd), fine gravel (FGraV), coarse gravel (CGraV), cobble (Cob), boulder (Bld), and bedrock (Bed).

DISCUSSION

Our findings quantitatively support previous observations that *R. sierrae* select stream locations with shallow, still, or gently flowing water and moderate cover (Zweifel, 1955; Mullally and Cunningham, 1956). More specifically, we found that adults (including subadults) preferentially selected low velocity and moderate depth microhabitats across the spring to fall seasons, with moderate to high percentages of total cover. We found that tadpoles selected very low velocity microhabitats, which supports observations from other studies that showed breeding sites with previous year tadpoles nearby were typically located in low velocity, shallow habitats (Brown et al., 2019, in this volume).

However, contrary to previous studies that suggested adults use predominantly coarse substrates, such as cobble and boulders (Mullally and Cunningham, 1956), our data showed adults occurred in both coarse substrates (cobble, boulder) and fine silt substrate, with few observations in sand and gravel. We found many adults basking on coarse cobble and boulder sized substrate, which was commonly available in our study sites, but adults were also found in microhabitats located in pools, side channels, and backwaters, which, during decreasing flows in late spring and summer, typically support deposition of finer bed material. Thus, when compared to the availability of substrates across our study sites, we found adults had a slight statistical preference for finer sized substrate material. While the observations of use

Table 6. Logistic regression modeling summary for microhabitat use by tadpoles of *R. sierrae* at Independence Creek (IND) and the South Fork tributaries (SFT & SFTT). Model estimates at each study site are mean values for 1,000 bootstrap iterations.

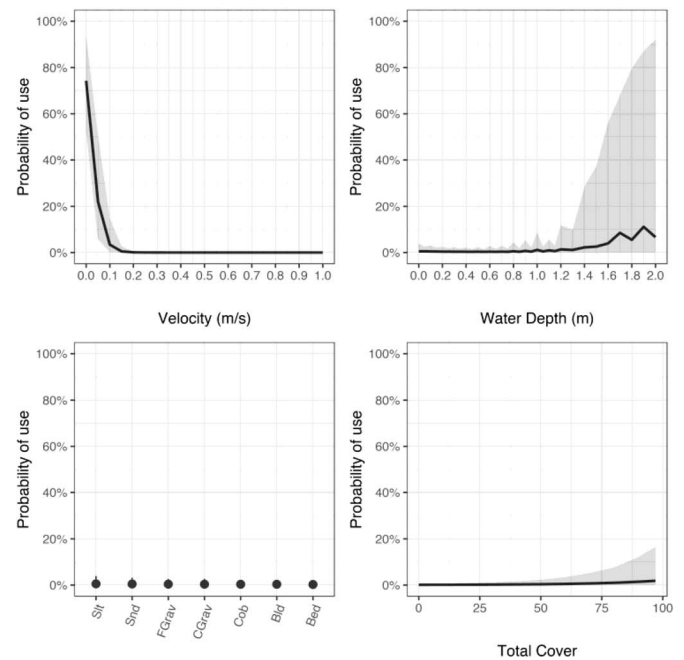
Site	Variables	Estimate	Standard error	Z-statistic	P-value
IND	Mid-column velocity	-51.968	19.158	-2.707	0.011
	(Intercept)	-4.066	3.167	-1.311	0.270
	Water depth	-0.485	2.522	-0.347	0.502
	Substrate	-0.020	0.253	-0.127	0.533
	Year	0.874	1.013	0.888	0.389
	Total cover	0.024	0.016	1.536	0.217
	Month	0.537	0.340	1.617	0.209
SFT & SFTT	Substrate	-0.414	0.217	-1.823	0.121
	Mid-column velocity	-55.124	32.635	-1.646	0.151
	Total cover	-0.001	0.016	-0.077	0.567
	(Intercept)	0.395	2.997	0.139	0.494
	Month	0.072	0.292	0.201	0.553
	Year	0.890	0.910	0.931	0.381
	Water depth	6.341	2.670	2.161	0.088

quantified in our study were based on visual encounter surveys, which may be biased towards exposed individuals that are more easily observed, a related telemetry study in two of the intermittent study sites commonly found telemetered adults in similar microhabitats to those observed in our visually based study (N. Keung, pers. obs.). Thus, we surmise that our results reflect the majority of microhabitat use by adults in our study sites.

The *post hoc* logistic regression models at Independence Creek and the South Fork tributaries highlighted the geomorphic variability that is common to streams across the Sierra Nevada. While the Independence Creek site models for adults and tadpoles produced similar results to the models across study sites showing water depth and velocity as the strongest habitat predictors, the models from the South Fork tributaries did not show velocity as a strong predictor for either adults or tadpoles. As flows decreased in the South Fork tributaries in spring, all available habitat had low velocities (Figs. 3, 10B). Thus, suitable low velocity conditions were highly available, and other habitat conditions (e.g., depth, cover) had more relevance for statistically separating use locations from available locations. Together then, this suite of models indicated that hydraulic conditions (velocity and depth) were the key predictors of microhabitat use, such that if depth and velocity were too high, the models predicted a low probability of use. However, when hydraulic conditions were suitable, cover and substrate conditions contributed to the suitability of habitat with their relative importance varying by site and by time.

To quantify habitat preferences that were common despite the geomorphic diversity across study sites, we created a set of habitat suitability relationships from the combined data for our study sites for those predictor variables shown to be most significant in the logistic regression modeling and exhibiting discrete thresholds or inflections in curves of probability of use. For adults, we observed changes in the probability of use for velocity and water depth, and quantified ‘high’ versus ‘low’ habitat suitability based on the 90th percentile of observed depth and velocity values. We defined highly suitable adult hydraulic habitat for this

A INDEPENDENCE CREEK



B SOUTH FORK TRIBUTARIES

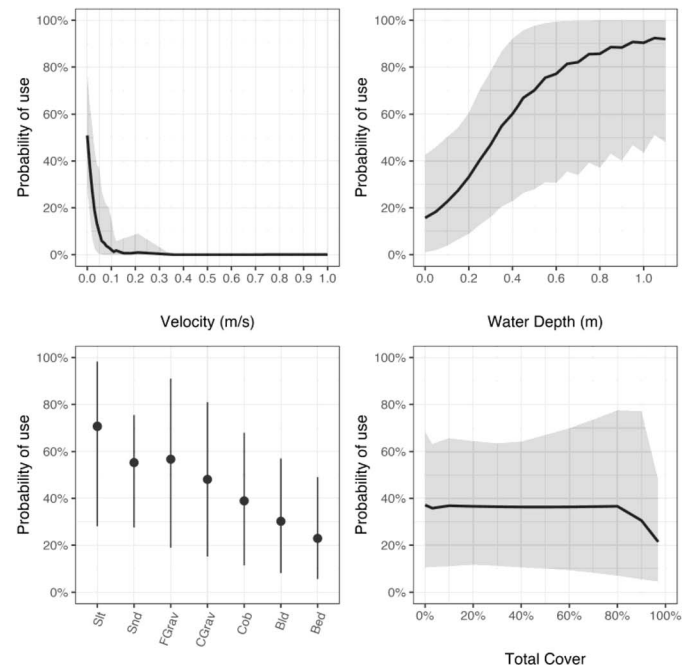


Fig. 9. Mean predicted probability of microhabitat use by tadpoles of *R. sierrae* for all possible values from a given predictor variable from the 1,000 bootstrapped logistic regression models at (A) Independence Creek and (B) South Fork Tributaries. Shading and bars represent 95% credible intervals. Substrate categories are silt (Slt), sand (Snd), fine gravel (FGrav), coarse gravel (CGrav), cobble (Cob), boulder (Bld), and bedrock (Bed).

analysis of our study sites at <0.3 m depth and <0.1 m s^{-1} . For tadpoles, we found a discrete threshold of velocity use at 0.1 m s^{-1} , and similarly quantified ‘high’ and ‘low’ suitable velocity based on the 90th percentile of observed use, such that highly suitable velocities were <0.01 m s^{-1} at our study sites. While these habitat suitability relationships are not

Table 7. Habitat suitability for adult use and tadpole rearing of *Rana sierrae* based on the 90th percentile of use values for those predictor variables shown to be most significant in the logistic regression modeling and exhibiting discrete thresholds of use at our study sites. 'High' suitability reflects the range of values for 90% of observed use across all study sites; 'Low' suitability reflects the range of observed values for the remaining 10% of observed use across all study sites. Water depth for tadpoles was not a significant habitat predictor for tadpole use across sites, so high versus low suitability were not quantified.

Lifestage	Count	Velocity (m s ⁻¹)		Depth (m)	
		High	Low	High	Low
Adults	286	<0.1	>0.1	<0.3	>0.3
Tadpoles	95	≤0.01	>0.01	n/a	n/a

applicable to other study sites without testing their transferability (e.g., Bondi et al., 2013), they did provide a quantification of suitable microhabitat conditions at our study sites for an evaluation of changing hydraulic conditions across seasons and water year types. We used the adult habitat suitability relationships to evaluate when and where suitable hydraulic conditions were occurring at our study sites, and to better understand why individuals may be selecting certain geomorphic units at the stream reach scale.

Based on our habitat suitability relationships, we found that suitable microhabitat conditions, specifically those with low velocities and low to moderate depths, can be found in a variety of stream channel morphologies and geomorphic units throughout the year. As stream flows gradually decreased from high discharge in spring to low discharge by late summer, hydraulic conditions changed accordingly at differing rates depending on channel morphology. Pools are maintained through time by scouring processes at high flows that create high depth and corresponding high velocities that mobilize and flush smaller substrates downstream (Thomson et al., 2001). As flows decreased at our pool sites, depths remained relatively high, but velocities decreased, allowing for smaller material to deposit. As a result, pools provided highly suitable habitat for adults and tadpoles in late spring and summer. Accordingly, *R. sierrae* selected pools more often

than expected on South Fork Rock Creek and associated tributaries. Furthermore, in these intermittent streams, the deeper channel conditions associated with pools provided the only remaining lentic water at the end of summer. Thus, *R. sierrae* may be seeking the hydraulic stability and suitability pools provide in higher gradient intermittent streams.

On Lone Rock Creek, adults selected higher gradient cascades and riffles, and were found less often than expected in pools. Unlike pools, cascades were dominated by larger substrates and had high velocities and moderate depths during high flows. As flows decreased into summer, however, velocities decreased as water moved between larger boulders rather than over them. In deeper pockets within cascades, water slowed, creating small areas of highly suitable hydraulic habitat with cover and basking sites due to immediately adjacent coarse substrate. The hydraulic variability inherent to cascades provided suitable low velocity habitat at different times of the year, providing an opportunity for additional suitable habitat beyond that provided by pools during summer low flows. As a perennial lower gradient stream, the associated diversity in hydraulic conditions throughout the seasons in varying geomorphic types at Lone Rock Creek may allow for greater use of habitat as climate conditions vary within and between seasons.

Although a low gradient site, Independence Creek had a high diversity in habitat availability across the main channel and side channels. As high flows in spring each year created limited suitability in the main channel geomorphic units, inundated side channels provided highly suitable habitat with lower velocities and moderate depths in a variety of pools, riffles, and runs. As flows decreased into summer and side channels dried out, hydraulic conditions in the main channel became more suitable. Accordingly, adults were observed in all available geomorphic units with little preference for particular types. Thus, in both Lone Rock Creek and Independence Creek, *R. sierrae* may be taking advantage of the greater microhabitat availability created across seasons as hydraulic conditions change across the diversity of geomorphic units present.

The strategy of using diverse stream habitat to find suitable microhabitat conditions across seasons is not unique to *R.*

Table 8. Proportion of use and availability of geomorphic units in each study site. Percent available values are based on proportion of stream length of each geomorphic unit type within each site. Percent use values are based on proportion of individuals observed within each geomorphic unit type at each site. Geomorphic units are ordered from highest to lowest gradient: Chute (CHT), Cascade (CAS), Step-pool (SPO), High Gradient Riffle (HGR), Low Gradient Riffle (LGR), Large Woody Debris Jam (LWD), Run (RUN), and Pool (POOL).

		CHT	CAS	SPO	HGR	LGR	LWD	RUN	POOL	χ^2	P-value
Independence Ck	Available	0.0	4.8	0.0	6.5	28.3	5.0	32.0	23.4	—	—
	Use: adult	0.0	7.4	0.0	8.8	35.3	1.5	22.1	25.0	5.49	0.36
	Use: tadpole	0.0	0.0	0.0	0.0	21.4	0.0	7.1	71.4	57.37	<<0.001
Lone Rock Ck	Available	0.0	9.2	0.0	1.4	15.6	0.3	40.2	33.4	—	—
	Use: adult	0.0	43.8	0.0	6.2	12.5	0.0	12.5	25.0	42.03	<<0.001
	Use: tadpole	0.0	0.0	0.0	16.7	0.0	0.0	0.0	83.3	99.56	<<0.001
South Fork Rock Ck	Available	1.1	62.2	4.1	0.0	8.0	0.0	4.7	19.9	—	—
	Use: adult	5.0	30.0	0.0	0.0	0.0	0.0	5.0	60.0	45.98	<<0.001
	Use: tadpole	0.0	0.0	0.0	0.0	0.0	0.0	0.0	100.0	n/a	—
South Fork Trib	Available	6.5	55.0	4.0	8.1	5.7	0.5	2.3	17.9	—	—
	Use: adult	7.1	28.6	11.2	1.0	0.0	3.1	3.1	45.9	37.32	<<0.001
	Use: tadpole	0.0	0.0	20.0	0.0	0.0	0.0	0.0	80.0	128.35	<<0.001
South Fork Tad Trib	Available	0.0	38.9	7.1	31.5	2.8	2.6	5.5	11.6	—	—
	Use: adult	0.0	26.0	35.6	12.3	0.0	1.4	0.0	24.7	43.33	<<0.001
	Use: tadpole	0.0	77.8	0.0	11.1	0.0	3.7	0.0	7.4	39.27	<<0.001

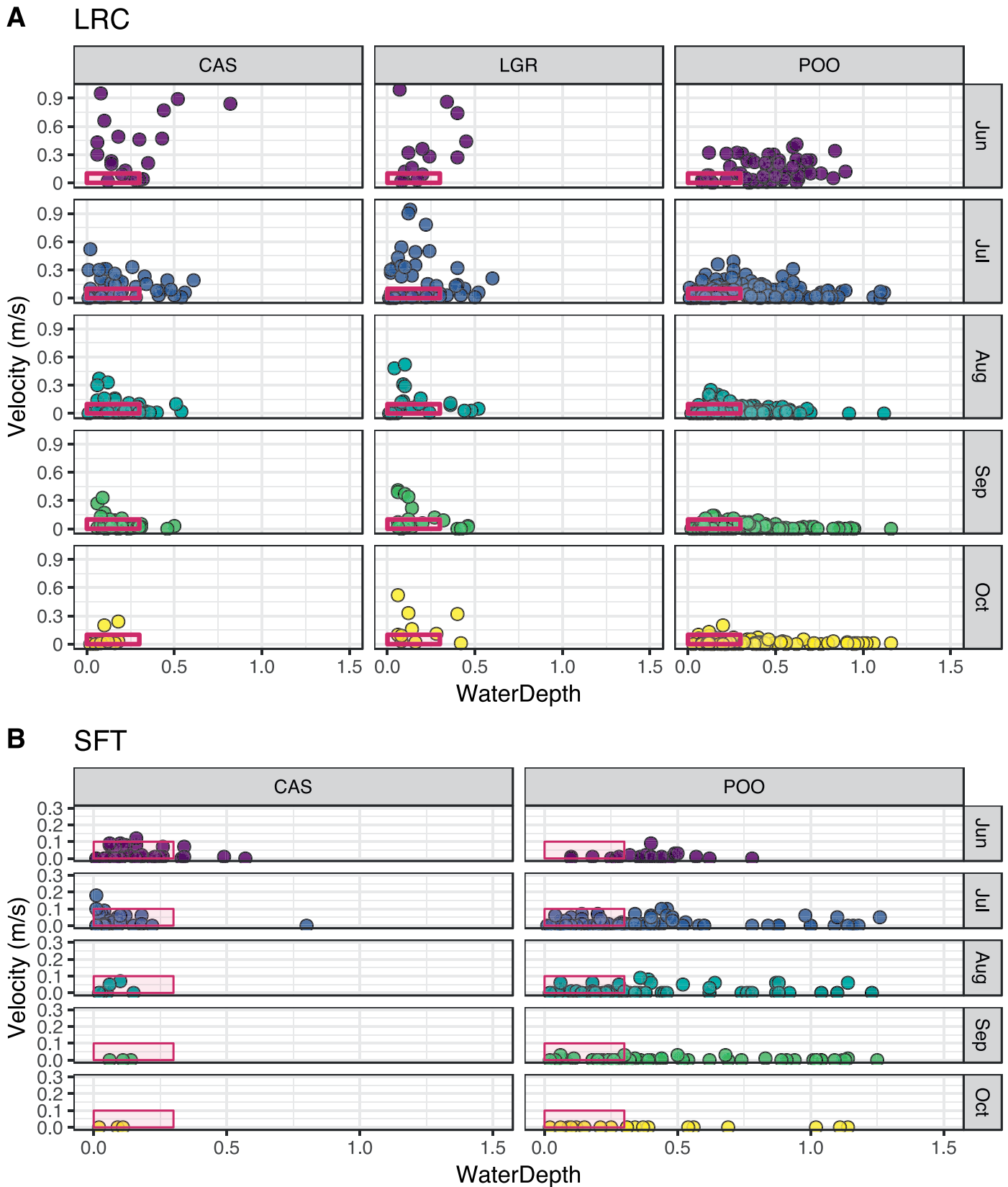


Fig. 10. Distribution of depth and velocity values over time within cascade (CAS), riffle (LGR), and pool (POO) geomorphic unit types at (A) Lone Rock Creek and (B) South Fork Tributary. Dashed and shaded box in lower left corner of each panel represents high suitability microhabitat for adults (includes subadults) of velocity $< 0.1 \text{ m s}^{-1}$ and depth $< 0.3 \text{ m}$.

sierrae. *Rana boylei* have been shown to select stream reaches that are more geomorphically heterogeneous and provide the variety of habitats needed by each lifestage within a shorter stream distance (Yarnell, 2008). Breeding and rearing habitats of *R. boylei* similarly occur in stream conditions with low velocities, moderate depths, and coarser substrates (Yarnell, 2013). Habitat suitability criteria developed for breeding and tadpole rearing of *R. boylei* define suitable velocity use below 0.55 m s^{-1} , and highly suitable conditions as $<0.16 \text{ m s}^{-1}$ (Bondi et al., 2013). These values are higher than the relationships quantified here, but tadpoles of *R. boylei* have evolved to withstand short-term velocity increases at the expense of energy for growth or increased predation risk (Kupferberg et al., 2011). As a larger bodied tadpole that requires multiple seasons to metamorphose, tadpoles of *R. sierrae* are likely less agile swimmers than tadpoles of *R. boylei*, and thus may be limited to very low velocity conditions. The lower velocity tolerances of *R. sierrae* may constrain the range of suitable habitat likely available at any given point in time as compared to *R. boylei*, but by using windows of opportunity when suitable conditions emerge in differing geomorphic units, *R. sierrae* may successfully persist in a variety of lotic-dominated environments.

The habitat suitability relationships quantified here are specific to our study sites, and additional data collected in other stream sites will increase our understanding of stream habitat preferences of *R. sierrae*. The number of tadpole observations in our study was limited due to repeat surveys of small populations, so additional information on rearing locations in other streams would help to better define suitable breeding and rearing conditions. Additionally, adults were occasionally observed in very shallow flowing habitats that we could not accurately measure for velocity. Future efforts that include stream habitat modeling or individual-based modeling may require additional information on quantitative thresholds to accurately determine impacts of changing habitat conditions on species response.

This study focused solely on physical habitat characteristics and preferences at the microhabitat and reach scales. Additional factors such as predation, water quality, food availability, or disease prevalence may affect habitat preferences as well. These other factors may be particularly relevant when suitable hydraulic habitat conditions are abundant, or they may interact with hydraulic conditions to increase or decrease habitat suitability. While cascades provide suitable low velocity microhabitat in summer during low flows, the higher velocities at high flows may help limit presence of fish or other predators of *R. sierrae*, potentially increasing the suitability of cascades. Similarly, while pools provide low velocity microhabitats year-round, they also more commonly support fish, potentially limiting the suitability of pools for breeding or rearing. The coarse substrates and higher dissolved oxygen levels associated with riffles typically support a greater abundance of benthic macroinvertebrates (Logan and Brooker, 1983), thus food availability for *R. sierrae* may be higher near riffles, adding benefits despite higher velocities. Additional study is needed to better understand how the complex interactions of multiple ecological factors with habitat in lotic systems support or affect *R. sierrae*.

In summary, our study findings quantitatively support previous observations that *R. sierrae* select shallow, slow-water, lentic-like habitats in the spring and summer seasons. Tadpoles in particular were found in microhabitats with very low to no velocity, similar to breeding habitat conditions observed in lentic-dominated systems. However, our data

show these preferred microhabitat conditions—specifically those with low velocities and low to moderate depths—can be found in a variety of lotic habitats throughout the year. In intermittent streams, *R. sierrae* may be seeking the hydraulic stability and suitability that pools provide into the low, disconnected flows of summer. In larger perennial streams, *R. sierrae* may be taking advantage of the greater microhabitat availability created across seasons as hydraulic conditions change throughout the diversity of channel morphologies and geomorphic units present. Similar to other ranid species like *R. boylei*, the ability to use windows of opportunity when suitable microhabitat conditions emerge in differing geomorphic units over time may allow *R. sierrae* to successfully persist in a variety of lotic-dominated environments. The inherent diversity of stream habitats across seasonal changes in flows may also provide *R. sierrae* with refugia as climate change alters precipitation and stream flow conditions in the future.

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