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FULL RESEARCH ARTICLE

Foothill yellow-legged frog breeding biology in a semi-regulated river, Humboldt County, CA

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River-breeding foothill yellow-legged frogs (*Rana boylii*) are endemic to California and Oregon. Across this wide geographic range, many populations have declined due habitat loss, non-native competitors and predators (e.g., American bullfrogs [*Lithobates catesbeianus*], Centrarchid fish), and disrupted water flow due to dams. Even when flow conditions are not extensively regulated, managers still require basic and region-specific information about the breeding biology of this species to prevent further decline. To document spatiotemporal dynamics of reproductive output during drought and high flow years, we surveyed a 13.5 km reach of the lower Mad River, Humboldt County, CA approximately 70 km downstream of Matthews Dam. We found relatively high densities of egg masses (39 to 59 masses / km). Egg masses were generally laid on small cobbles (mean ±SE diameter = 11 ± 0.24 cm) at depths between 0 and 20 cm, and 95% of egg masses were laid within 6 m of the wetted edge. Egg masses were disproportionately found in the tailouts of fast runs and glides, and found less often than expected in side arms, runs, and riffles than would be expected by chance. Breeding timing appeared to be more related to rapid decreases in stream flow variance than air temperature. Taken with previous information about the species, our results suggest that *R. boylii* rely on multiple cues to initiate breeding. Our results can be used to help inform breeding timing and habitat use by *R. boylii* breeding under natural flow regimes in Northern California. Our recommendations for future research include further investigating upland habitat use by post-metamorphic life stages factors that influence breeding site selection.

Key words: amphibian, flow rate, land use, oviposition site selection, *Rana boylii*, river-breeding frog, tributaries

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River ecosystems can be highly vulnerable to human disturbances, which often affect the survival and spatial distribution of aquatic species (Bondi et al. 2013). Anthropogenic activities, such as water diversion, hydroelectric power generation, flow regulation, and other habitat modifications alter the regular flow regimes of rivers and streams, which can cause changes in species assemblages and biodiversity loss (Kupferberg 1996; Femmer 2002; Tonkin et al. 2018; Best 2019). Dam construction and operation can disrupt natural water flow cycles and pose a threat to river-breeding and flood-plain-breeding frogs (Eskew 2011; Kupferberg et al. 2012; Peek et al. 2020). In particular, dam operations to generate electricity can affect the reproductive success of amphibian populations, as egg masses are subject to scouring and stranding from irregular flow timing (Wheeler and Welsh 2008). Flow rates from dams can fluctuate seasonally, monthly, daily, sporadically, or remain static depending on the type of dam and management plan (Kupferberg et al. 2011). Changes in flow regime from historical norms are dependent on multiple factors, including the purpose of damming (i.e. hydroelectric, reservoir, and flood control), size of and distance to the dam, and number of downstream tributaries (Bunn and Arthington 2002). Here, we define "semi-regulated" to describe rivers that are dammed but generally mimic historical seasonal patterns of flow timing and magnitude. Understanding the breeding ecology of sensitive species in semi-regulated rivers can offer valuable insight into beneficial flow regimes in regulated systems.

Foothill yellow-legged frogs (*Rana boylii*) are obligate stream breeding ranid frogs that are particularly vulnerable to perturbations from river and stream flow regulation. Through much of their native range in California and Oregon, *R. boylii* are experiencing population declines (CDFW 2019). Several regionally distinct genetic clades were recently listed under the California Endangered Species Act, including the lineages in the Southwest/South Coast, West/Central Coast, and East/Southern Sierra clades (endangered) and the Northeast/Northern Sierra and Feather River clades (threatened; CFGC 2020). While the California Fish and Game Commission determined that listing of the Northwest/North Coast clade was not warranted, this clade is still designated as a Species of Special Concern in the state. *Rana boylii* population declines have been attributed to anthropogenic disturbances such as river modifications from damming and introduction of invasive species including the American bullfrog (*Lithobates catesbeianus*), signal crayfish (*Pacifastacus leniusculus*) and largemouth bass (*Micropterus salmoides*) (Wiseman et al. 2005; CFGC 2020).

Rana boylii relies on key habitat features for reproduction in lotic environments, including low flow velocity sites and cobble-sized substrate for oviposition sites (Rombough and Hayes 2005; Lind et al. 2016). Eggs and tadpoles are most successful under natural seasonal flow patterns wherein rivers flow quickly during wet winters and slowly during dry summers (Kupferberg 1996; Lind et al. 1996). *Rana boylii* typically initiates breeding in late spring, when temperatures increase, and river flow rates have declined and stabilized (Wheeler et al. 2018). Breeding season duration is site specific and variable by population and year, spanning from 14 to 31 days (Storer 1925; Zweifel 1955; and Van Wagner 1996). Nonetheless, *R. boylii* breeding appears to be relatively synchronous within a population compared to other ranids such as lentic breeding northern red-legged frogs (*R. aurora*; Wheeler et al. 2018). *Rana boylii* can delay oviposition in response to increased rain during the breeding season, which may allow for higher reproductive success by avoidance of egg mass scouring during late-season flooding events (Kupferberg 1996; Ashton et al. 1998; Bondi et al. 2013). Additionally, oviposition has been correlated with increasing air temperatures, a proxy for warmer water temperatures that likely facilitate successful reproduction (Wheeler et al. 2018) and presumably correspond with lower summer flows. While tadpoles survive higher flow rates than egg masses (Lind et al. 1996), larval growth and survival may be negatively impacted by flow rates that are exceptionally high or that occur late in the breeding season (Kupferberg et al. 2011). Metamorphosis typically occurs three to four months after hatching, although the timing of metamorphosis is dependent on water temperature and food availability (Ashton et al. 1998). A central concern for conservation of *R. boylii* depends largely on understanding the impacts of regulated flow regimes on instream habitats, particularly during the species' reproductive and growing seasons.

The terrestrial environment surrounding rivers may also negatively affect *R. boylii* populations, and spatial patterns of extirpation are consistent with a habitat destruction hypothesis (Davidson et al. 2002). Previous work has found that preserving a riparian buffer around water sources is important for amphibian conservation (Semlitsch and Bodie 2003; Marczak et al. 2010). Urbanization and human encroachment pose a threat to over one-third of the world's amphibian species as a result of habitat loss, fragmentation, and degradation of available habitat (Hamer and McDonnel 2008). However, riparian habitats are often overlooked in amphibian conservation even though they are vital for the completion of life stages for many species (Semlitsch and Bodie 2003). With the rate of urbanization rising on a global level it is necessary to consider the implications of land use changes on neighboring riparian and aquatic habitats (Alig et al. 2004).

The Mad River and its watershed, in Humboldt County, California, have been altered by agriculture, urbanization, and the installation of the Matthews Dam, which captures approximately 25% of the total upstream watershed runoff. Releases have been designed to maintain aquatic habitat for listed salmonids during low-flow months, typically in late summer and early fall (HBMWD 2004). Despite having some hydroelectric capacity, the flows from this dam are mostly regulated by overflow, creating relatively natural seasonal flow patterns downstream. In addition, much of the lower Mad River is surrounded by agriculture and urban development.

Given that the Matthews Dam provides a relatively natural flow regime for oviposition sites, investigating suitable breeding habitat along the Mad River may be useful for informing future management strategies to conserve *R. boylii* in more regulated systems. In addition, uncertainty in future water availability caused in part by recent variation in precipitation, including a historic multi-year drought, is a major driver of environmental politics and management in California (e.g., Doremus and Tarlock 2008). In this study, we aimed to incorporate the differences of water availability during years with normal flow (2011), drought (2015), and high flow during El Niño Southern Oscillation (2016) in an effort to provide guidance on river conditions that support reproduction of *R. boylii.* Additionally, this study aimed to describe the spatial and temporal patterns of oviposition in relation to adjacent terrestrial habitat and seasonal temperature patterns to offer insight into the role that riparian buffers play in supporting the adult life stage of *R. boylii*.

To address these issues, we explored three complementary hypotheses regarding oviposition sites on the lower Mad River. First, we assessed the impacts of flow rates and air temperature on oviposition timing within years by identifying the stability of flow rate during the breeding period as well as the number of days since peak flow. We expected to find a pattern of early oviposition during low flow rates (drought year), and later oviposition during years with high flow rates. Second, we compared land-use types and river tributaries' spatial relationship to oviposition sites, predicting that oviposition may be associated with riparian areas, closer to tributaries, and further from urban areas. Finally, we identified spatial patterns of oviposition sites within the Mad River, describing distance to wetted edge, depth of egg mass or larvae, and river features used for oviposition, and we predicted these physical parameters would be similar to those used by frogs in other regions (Bondi et al. 2013).

METHODS

Study Area

We conducted fieldwork in a 13.5-km reach of the Mad River (between 40.91, -124.01 and 40.84, -123.98, NAD83) approximately 70 km downstream from Matthews Dam in Humboldt County, California (Fig. 1). Two major tributaries join the Mad River below the Dam, Maple Creek and the North Fork Mad River. We completed surveys during the breeding season in three years (2011, 2015, 2016). We classified 2011 and 2016 as high flow years, whereas 2015 was classified as a year of peak drought. Annual mean discharge rates (in cubic feet per second; cfs) during study years varied from 770–1945 cfs (USGS NWIS 2017). Annual discharge rates were available for 2008–2016 and ranged from 410–1945 cfs, indicating that our study years spanned the range. Land use of the floodplain near the river consisted primarily of small-scale agriculture, rural residential use, and urban development.

Field Surveys

We conducted field surveys in 2011, 2015, and 2016. We timed surveys based on the estimated peak egg mass deposition, which was variable between years. Therefore, to determine the timing of peak *R. boylii* breeding activity, and initiation of survey, we relied on spot checks at reliably occupied upstream sites as the breeding season approached (Bourque and Bettaso 2011). We surveyed the entire study area once per year. To complete visual encounter surveys, two or more biologists walked the wetted edge, either upstream or downstream, depending on access points. We counted all egg masses, assigned an approximate embryonic development stage (i.e., Gosner stage, Gosner 1960) and recorded egg mass location using a global positioning system (GPS) unit. We grouped Gosner stages into four approximate categories: round (1–14), bean (15–18), tail (19–21), and hatching (i.e., when larva where observed on/at the egg mass). Additionally, in 2015, we recorded microhabitat variables for each egg mass, including depth of egg mass, substrate size (median diameter), and distance to wetted edge.

Oviposition Timing

To study the effect of flow rate on *R. boylii* breeding in the lower Mad River, we estimated breeding season start and end dates, and compared these date ranges with discharge rates during years of high (2011 and 2016), and drought (2015) flows. We estimated oviposition start date (beginning of breeding season) as 21 days prior to the first observation of a 'hatching' (latest stage) egg mass. Estimated breeding season end date was estimated as 21 days after the last observation of a 'round' (earliest stage) egg mass. To quantify the relationship between flow rate and oviposition date, we estimated standard deviation of daily discharge rate, as measured at the USGS Mad River Station near Arcata (USGS NWIS

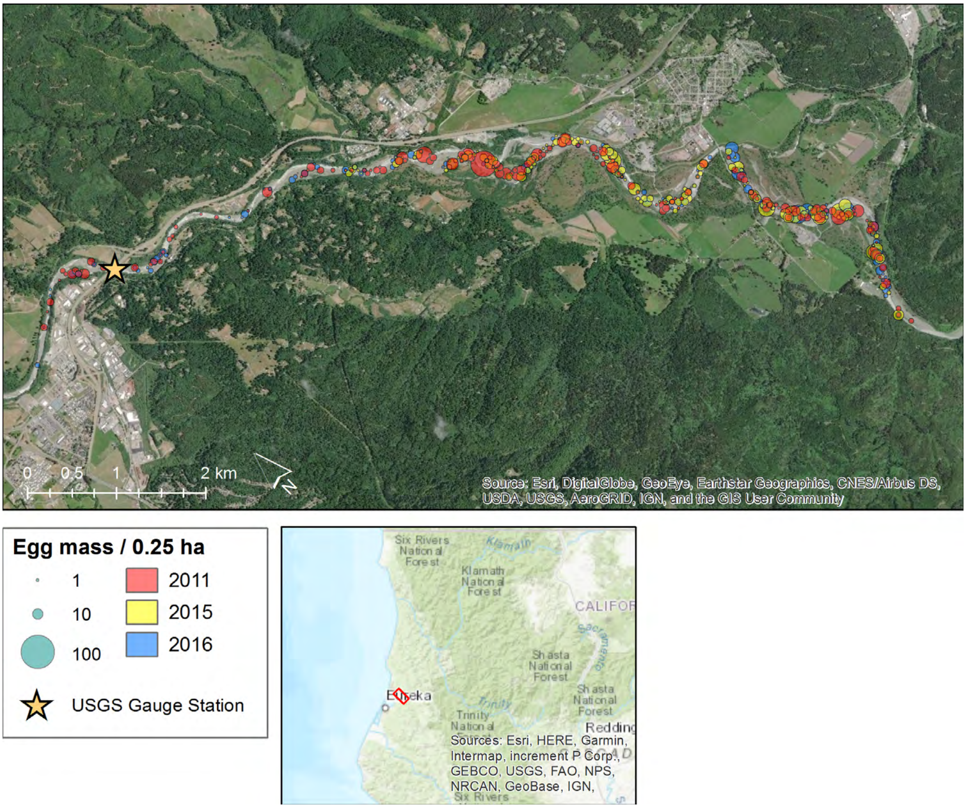

Figure 1. Study site along the lower Mad River, Humboldt County, California with foothill yellow-legged frog egg mass locations from three survey years.

2017), using a moving time window of 21 days. While precise estimation of breeding onset is difficult using this backdating approach, we selected a window based on development rates in a lab setting with mean air temperatures comparable to the conditions during the breeding season in our study area (Kupferberg et al. 2011). We then used piecewise regression to identify the breakpoint in the standard deviation of flow rate (Toms and Lesperance 2003), after which we compared breakpoints to the estimated oviposition start date. We also assessed whether pulse flows that may have resulted in decreased survival occurred during the breeding season time period. We compared the log ratio of daily maximum and minimum discharge to survival rates measured in Kupferberg et al. (2012).

To estimate the effects of temperature on breeding initiation, we compared air temperature within and between years because water temperature was not available. Relationships between air and water temperature are generally correlated, although not necessarily 1:1 (e.g., Morrill et al. 2005). We acquired daily maximum, minimum, and mean temperatures from the National Weather Service's weather station on Woodley Island, Eureka, California (USW00024213). We used ANOVA to compare minimum and maximum temperatures during estimated breeding season, one week prior and post estimated breeding start date, and mean temperatures between 15 March and 15 April during each study year and pooled across years.

Oviposition Site Selection

To investigate the influence of adjacent terrestrial land use on oviposition site selection, we digitized the area around the study reach using NAIP imagery (US Department of Agriculture 7 June 2014, 1 m resolution), dividing it into six land types. These types included the following: agriculture, developed, open areas, ponds, trees, and the river (Table 1). We digitized these areas by relying on our collective knowledge of land use in the study area. We defined river habitat as anywhere within the bankful margin (i.e., the area where water is contained within the channel under most flow conditions, and where flows do not connect with the floodplain). Previous research has found that amphibians are most successful when there is a 159 to 290 m riparian buffer around aquatic habitat (Semlitsch and Bodie 2003). With this in mind, we digitized all land within 1 km of the survey area. Egg masses tended to be concentrated within particular sections of the river. To control for spatial autocorrelation among points, we calculated Ripley's K to identify a distance at which egg mass density was no longer correlated (Bivand et al. 2008). We then created a raster of egg mass density using a cell size (50 m) equivalent to the minimum distance that resulted in no significant spatial autocorrelation.

Next, we used generalized linear models with a Poisson link to examine the relationship between egg mass density and percent of each land use type at different distances from the egg masses. For each survey year, we created multiple models based on different buffer distances (from 100 m to 1,000 m, in intervals of 50 m) around each cell to identify the distance from egg masses that best explained variation in egg density. For example, for the 100 m buffer, we calculated percent of each of the six land use types within 100 m of each 50m cell and created a generalized linear model to predict the relationship between the two. We created separate models for each buffer distance. These distances represented different "hypotheses" related to the most important spatial scale to explain difference in egg mass density. Models were ranked using Akaike's Information Criterion corrected for small sample sizes ("AICc") (Burnham and Anderson 2002). We then assessed the relative contribution of different land use types to explain the spatial variation in egg mass density. We expected that egg mass density would be positively correlated with trees and undeveloped open space and negatively related to agriculture and developed areas.

Finally, we examined oviposition microhabitat selection within the river in two ways. First, in 2015, we measured three variables at every egg mass: water depth, distance to wet-

Table 1. Land cover/land use categories used to digitize terrestrial areas surrounding the lower Mad River.

Type	Description
Riparian	Low lying vegetation and broadleaved trees near bodies of water
Trees	Mainly conifers. Other trees indistinguishable between conifers and riparian
Agriculture	Actively or recently farmed
Open	Meadows, lawns, pastures, and areas that may have been previously farmed but had no observable signs of agriculture
Ponds	Standing water
Developed	Pavement, houses, and other signs of human habitation or development
River	Bankful margin of the Mad River

ted edge, and substrate size. We summarized these data in relation to growth stage. Next, we digitized the river within the survey area using standard classifications for river features believed to influence *R. boylii* oviposition sites: backwater, disconnected pool, fast run, fast run tailout, glide, rapid, riffle, riffle tailout, run, run tailout, and side arm (Hauer et al. 2009). We acquired georectified aerial imagery generated by National Marine Fisheries Service from flights flown in May or June of each year of the study. Resolution and precision were <0.5 m (i.e., the imagery was more precise than the GPS locations of the egg masses themselves). Each mapped egg mass was assigned the river feature within which it fell, or was closest to, if the egg mass fell outside of the mapped area. We then calculated total percent area of each river feature represented within the survey area and compared these percentages with the percent of total egg masses found in each. Following standard habitat selection theory, we assumed that river features with a higher percentage of egg masses than was available in the area represented features "selected" by the frogs, with areas under-represented by egg masses were "avoided." We expected egg masses to be concentrated in "slower" parts of the river (disconnected pools, backwaters, and tailouts), and that these concentrations would be consistent across years.

RESULTS

We observed 2,308 egg masses total during our three years of sampling in the study area (Fig. 2; Table 2). The spatial distribution of these egg masses varied considerably across the study reach and egg mass density ranged from 0.004/m^2 to 0.024/m^2. We detected particularly high egg mass densities in a few locations (e.g., around the confluence of the north and south forks of the Mad River (Fig. 2), which remained consistent across the three study years. Egg mass density was lower toward the downstream end of the study area during the drought year (2015) compared to high flow (2011 and 2016) years.

Oviposition Timing

Mean daily discharge rates (in cfs) in the lower Mad River peaked many times throughout the winter season, while the onset of spring brought a final peak and subsequent decline (Fig. 3). In 2011 and 2016 (high flow years), the estimated oviposition start date occurred 26 and 31 days after a sharp reduction in the standard deviation of flow rate (Fig. 3). However, in 2015 (drought year), flow rate stabilized much earlier in the year and the estimated oviposition start date occurred approximately seven weeks after this breakpoint. The estimated breeding season started and ended earlier during the drought year (April 17 to June 9) compared to the high flow years of 2011 (May 25 to July 9) and 2016 (May 3 to June 24). Flow on the estimated breeding start date was 844, 437 and 551 cfs in 2011, 2015 and 2016, respectively, and it declined to 182, 78, and 102 cfs by the estimated breeding end. During the estimated breeding seasons, the min:max discharge ratio did not exceed one, indicating that there were no post-breeding pulses that would negatively impact survival. Across all three years, the onset of the breeding season was marked by significantly warmer ambient air temperatures compared to the week prior to onset and between March 15 and April 15. Across all three years, there was a particularly significant increase in the daily minimum temperature, from 7.4° C one week prior to breeding onset to 8.7° C one week after the estimated onset (Appendix Table 1).

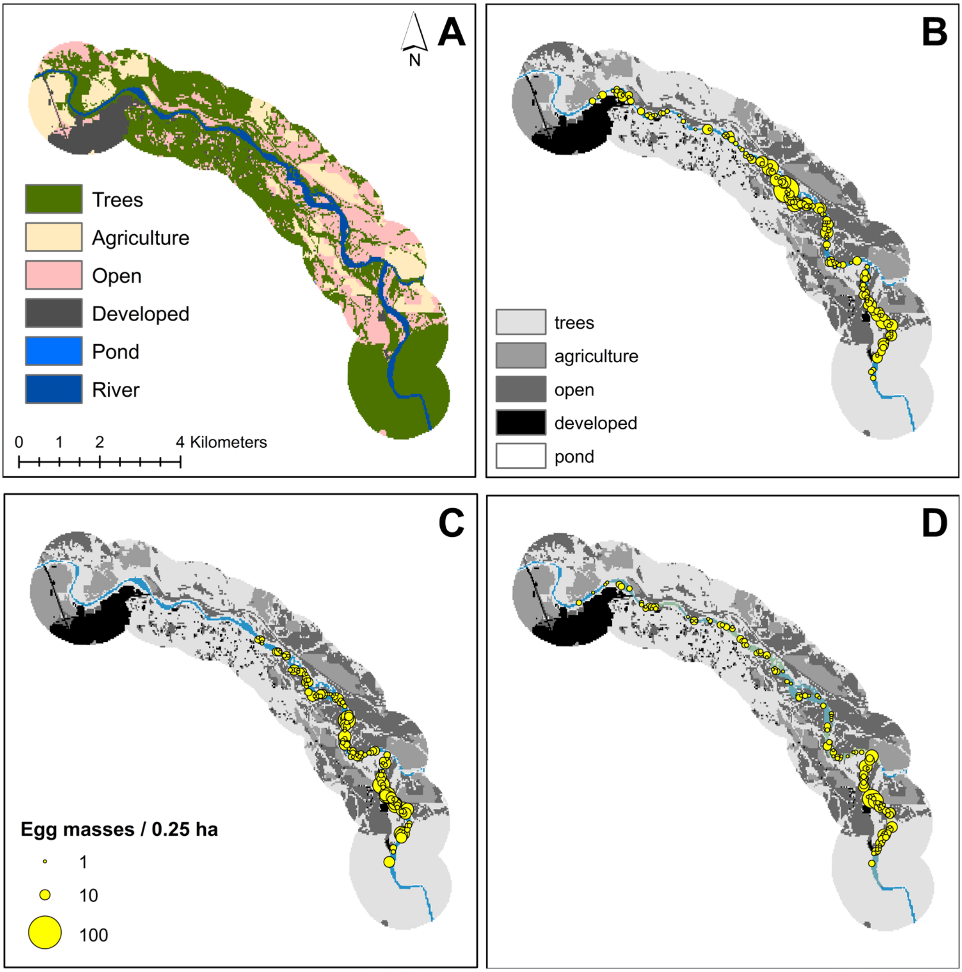

Figure 2. Land use / land cover types along the lower Mad River, Humboldt County, California (A); foothill yellow-legged frog egg mass densities in 2011 (B), 2015 (C), and 2016 (D).

Oviposition Site Selection

The buffer distance that best explained variation in egg mass density compared to surrounding land use types varied by year (Appendix Table 2-4). In 2016, the best model included a buffer distance of 400 m; in 2011, 450 m; and in 2015, 900 m (Table 3). Selection of land use types did not neatly fit with our original expectations. In all three years, the percent cover of trees within the buffered area was negatively related to egg mass density. By contrast, the percentage of agriculture, open areas, and ponds were all positively related to egg mass density. In 2011, developed area was positively correlated with egg mass density, but in 2015 and 2016 it was negatively related.

Egg masses were almost exclusively found between 1 and 10 m from the wetted edge and between 0 and 20 cm in depth (Fig. 4), with 95% found within approximately 6 m of the wetted edge. Mean substrate diameter was 11 cm (min = 2 cm, max = 120 cm, 25% =

Table 2. Results of egg mass surveys in lower Mad River, Humboldt County, CA, during peak breeding season across three years.

Year	Survey Dates	Number of Egg Masses Observed	Egg Mass Density per Kilometer
2011	June 14 - June 17	795	59
2015	May 7 - May 22	986	73
2016	May 23 - June 3	526	39

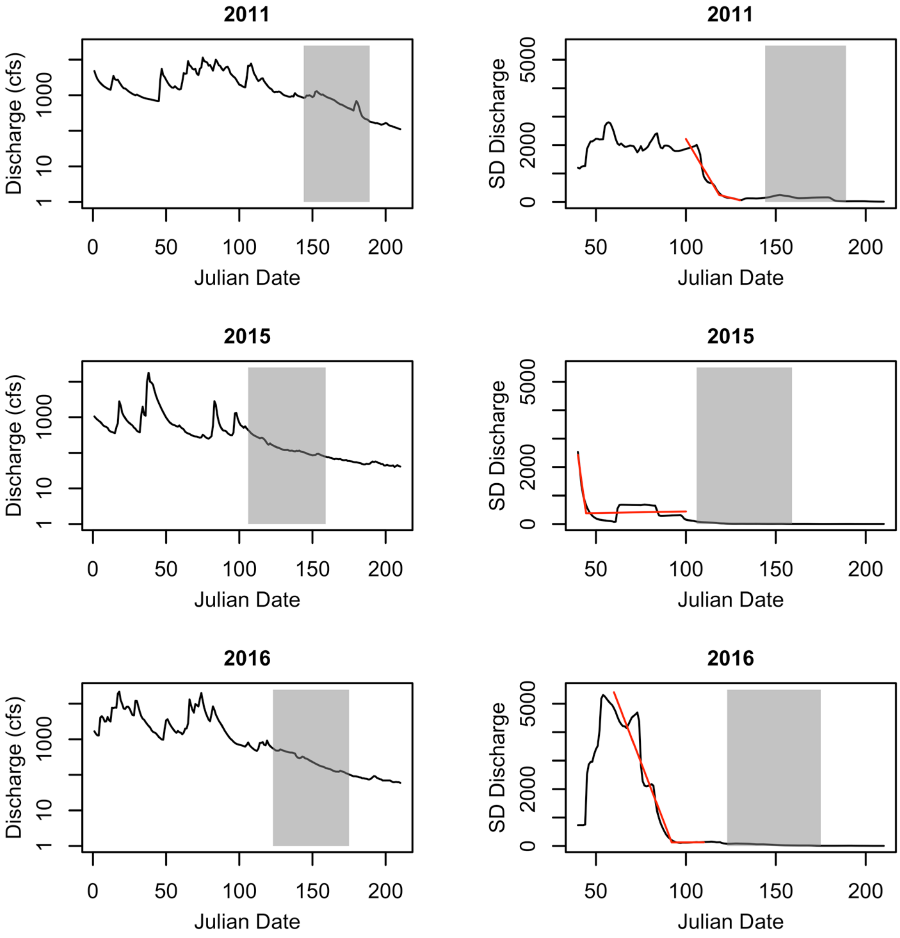

Figure 3. Flow rate (mean, left and standard deviation, right) at the Mad River Gauge Station, Arcata, California from January 1 to July 31 during years of foothill yellow-legged frog survey. Gray rectangles indicate estimated breeding season, defined as a 21-day hatching period on either side of survey dates. Red line indicates the piecewise linear regression and breakpoint. Standard deviation was calculated within a 21-day moving window.

Table 3. Coefficient estimates for the top model from each year relating to foothill yellow-legged frog egg mass density to percent cover of surrounding land use types in the lower Mad River, California (standard error given in parentheses) using buffer distances that best explained spatial variation in egg mass density for that year.

Year	Best supported buffer distance	Intercept	Trees	Agriculture	Open	Developed	Pond
2011	50 m	-5.15 (0.33)	-1.57 (4.75)	-4.74 (1.13)	8.67 (0.56)	NA	7.45 (0.47)
2015	900 m	-4.98 (0.33)	-16.45 (1.39)	9.16 (1.87)	4.82 (0.63)	-920.93 (128.6)	61.96 (5.27)
2016	950 m	-2.76 (0.32)	-7.34 (1.14)	4.29 (1.34)	0.89 (0.80)	-1,975.72 (226.65)	37.47 (6.36)

7 cm, 75% = 14 cm). Overall, egg masses were significantly, disproportionately found in the tailouts of fast runs and glides, but under-represented in side arms, runs, and riffles ($\chi^2 = 392.03$, $df = 10$, $p < 0.001$) (Fig. 5).

DISCUSSION

In this study, we examined spatial and temporal distribution of *R. boylii* egg masses across two high flow (2011, 2016) and one drought year (2015). In each of the three years, onset of breeding occurred more than a month after the final major pulse of rainfall, and minimum air temperatures one week after estimated breeding onset were significantly warmer than previous weeks. High egg mass densities occurred closer to agriculture, open areas, and ponds, and further from trees and developed areas.

Egg mass density has been used as a metric of population size in *R. boylii* and unregulated rivers maintain a more consistent level of egg mass density (Kupferberg 2012). Egg mass densities calculated over the total length of our study reach (39 to 59 egg masses/km, Table 2) were comparable to density estimates from the South Fork Trinity River (35 to 47 egg masses/km) and Hurdygurdy Creek (18 to 30 egg masses/km) in northern California (Lind et al. 2016). However, there was substantial variation along the reach, with egg mass densities approaching 200 / km in certain 1 km stretches of the river (Fig. 2).

Average substrate size at observed egg mass in our study (11 cm) were comparable to a study in the South Fork Trinity River and Hurdygurdy Creek, which found the majority of egg masses on cobbles between 6.4 and 25.6 cm in diameter (Lind et al. 2016). However, our results differ from a study in the Sierra Nevada, where egg masses were observed fairly equally on cobble and boulder substrate (Yarnell et al. 2011). This could be a result of the difference in stream habitat characteristics between higher elevation mountain and coastal drainages, but it may also reflect differences in traits between *R. boylii* clades.

Results from the broader analysis of habitat selection were inconsistent with previous findings on *R. boylii* breeding habitat. Unexpectedly, we found that egg mass densities were higher with greater percent cover of agricultural areas. We suspect this is most likely

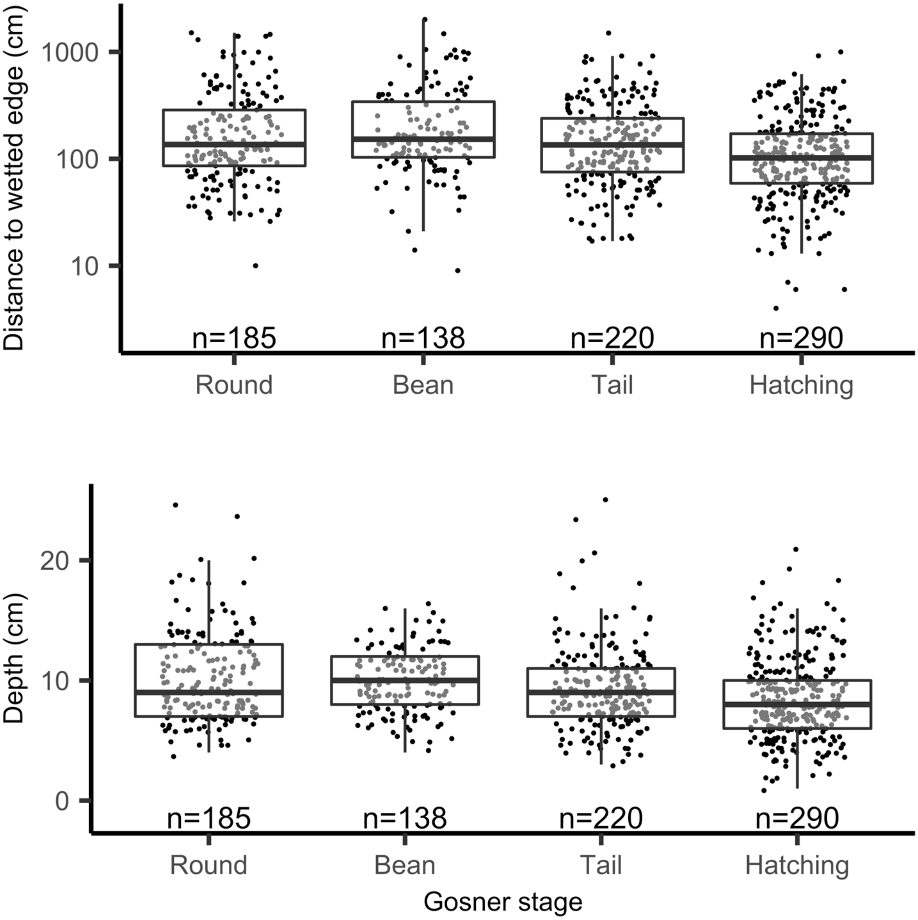

Figure 4. Box plots representing distance of foothill yellow-legged frog egg masses from wetted edge (top) and river depth at egg masses (bottom) on the lower Mad River, Humboldt County, California at time of survey in 2016.

a coincidence – riparian vegetation may have much better explanatory power, but we did not have reliable spatial data to measure riparian vegetation within the study area. There may have been other, more localized factors that contributed to high egg mass density in areas that happened to fall closer to agricultural areas – for example, flatter, wider reaches preferred by *R. boylii* for egg mass deposition (Lind et al. 2016) may have been more likely further downstream, where the majority of agricultural land use is found.

Our results on the microhabitat conditions for oviposition match with previous literature. Lind et al. (2016) found a narrow range of oviposition microhabitat characteristics, with *R. boylii* selecting wide, shallow segments of the stream with low water velocity and cobble-sized substrates for oviposition sites. Virtually all the egg masses we found were in depths between 0 and 20 cm, although some of these were up to 10 m from shore – in other

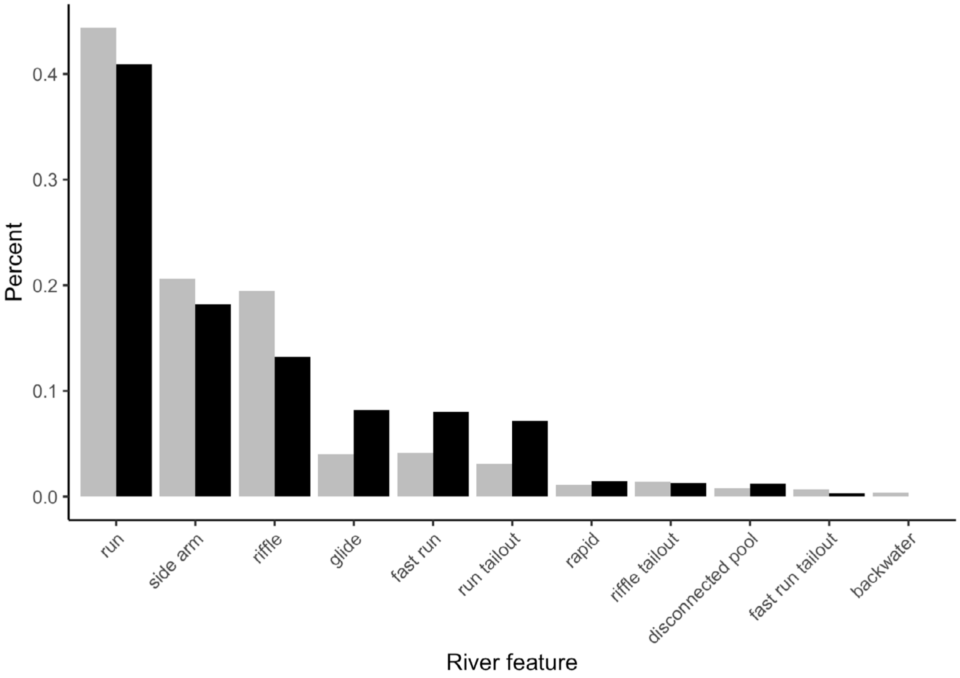

Figure 5. Left: proportion used (black) vs. available (gray) for foothill yellow-legged frog oviposition sites among river features on the lower Mad River, Humboldt County, California in 2011, 2015, and 2016 combined. Right: difference in used and available proportion of river features for 2011 (light gray), 2015 (dark gray), and 2016 (black), ordered from most to least used; positive percent suggests selection of that feature for oviposition, negative percent suggests avoidance, order from most to least selected.

words, wide, shallow segments of the river. We noted a general lack of stranding in this study, consistent with the beneficial stream morphology and limited anthropogenic water development in the lower Mad River.

Oviposition occurred earlier in years of low base flow (2015) compared to years of higher discharge (2011, 2016), consistent with *R. boylii* on the South Fork Eel River (Kupferberg 1996). Onset of breeding season in relation to flow patterns suggests *R. boylii* use periods of steady or decreasing flow rates as a cue to initiate oviposition (Kupferberg et al. 2012). As demonstrated in this study, the start of breeding approximately two weeks after flow stabilization suggests that durations of low variation in flow signal adequate oviposition conditions. However, during the drought year of 2015, flows stabilized more than seven weeks prior to initiation of oviposition – breeding onset is therefore likely triggered by multiple environmental cues. For example, in dry water years, when discharge is limited and flows decrease earlier than during more average water years, *R. boylii* may also use day length or water temperature cues to initiate breeding.

Similar to Kupferberg (1996), air temperature during the first week of oviposition were significantly warmer than previous weeks, with a notable increase in average minimum temperature one week after our estimated breeding onset compared to the week prior. However, 2015 was a warm year and air temperatures in mid-February were similar to temperatures at 2011 and 2016's breeding onset in April. The early increase in temperature and steadying flows during this extreme drought may have exceeded the species' plasticity in breeding timing, or *R. boylii* may rely on multiple cues to initiate breeding. Further, our estimate of breeding onset is based on backdating from peak egg mass surveys. It is likely that some frogs began breeding earlier than our breeding start estimate because development times are temperature dependent, thus backdating from Gosner stages is only an estimate of oviposition dates. Finally, estimates of water temperature rather than ambient air temperature would have been more useful to estimate breeding onset and development time, as well as potentially more informative to explain breeding timing. Surveys to determine first date of oviposition may provide further insight into the relationship of flow, temperature, and breeding.

Increased flows due to dam release during late spring and summer could have a negative effect on the density and survival of *R. boylii*, as these flows do not coincide with natural patterns and do not provide environmental cues (Kupferberg 2012). Late-season releases from the Matthews Dam, however, seem to be buffered at our study site by distance from the dam and incoming tributaries below the dam, as summer peaks were not visible in flow data from the USGS Mad River gauge station near Arcata (USGS NWIS 2017). We found that there were no late season pulses that would impact egg or tadpole survival in any of the three years (Lind et al. 1996; Kupferberg et al. 2012), suggesting Matthews Dam did not negatively impact frog breeding in our study area during these three years.

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