

NOVEL ASPECTS OF OVIPOSITION SITE PREPARATION BY FOOTHILL YELLOW-LEGGED FROGS (*RANA BOYLI*)

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Recently, Wheeler and others (2003) reported a heretofore-undescribed behavior wherein female foothill yellow-legged frogs, *Rana boylei*, scrape the rocky substrate with their hind feet prior to oviposition. They observed that this behavior loosened algae and sediment and postulated that it could enhance the ability of egg masses to adhere to the substrate. Based on 2 episodes at a site in northwestern California, their observations provide a 1st glimpse of this behavior. Here, we add serial observations of this behavior by 2 additional female *R. boylei* from western Oregon. These observations increase our knowledge of substrate preparation behavior and suggest that females of this species evaluate oviposition site quality.

Observations were made in June 2004 during an ongoing study of the northernmost extant population of *R. boylei* (Rombough 2002), the last known population remaining in the Willamette hydrographic basin (Borisenko and Hayes 1999). This site is located on a sharp (approximately 120°) bend of the South Santiam River (Linn County, Oregon; 44°40'97"N, 122°56'54"W [datum: WGS84]; elevation 192 m). The substrate is primarily hard volcanic tuffs, which form a relatively flat bedrock surface approximately 400 m long and up to 150 m wide; this surface is scoured bare of nearly all loose rock <0.5 m in diameter. Seams of soft conglomerates in this bedrock have eroded, leaving numerous troughs and scour pools, the largest of which are lined by clumps of sedge and often contain smaller cobble and gravel. Oviposition by *R. boylei* takes place exclusively in a few off-channel pools and troughs with reduced flow velocities, decreasing the likelihood of egg scour (Rombough 2002; see also Kupferberg 1996a; Lind and others 1996).

All observations reported here occurred immediately before and during oviposition. Ob-

servations took place in shallow (0.22 to 0.27 m) water near the edge of an 8-m-diameter scour pool where frogs have bred during each of the past 5 years (from 2000 to 2004). Located along the west margin of the active channel, the west side of the pool had a soil and riprap bank overhung by bigleaf maple (*Acer macrophyllum*). At least 40 m of bedrock flat separated the east side of the pool from the perennial river channel. During the breeding season, male *R. boylei* generally approach the site from the east, whereas females usually enter from the west, from the direction of the forested bank. On this occasion, CJR had the opportunity to observe frogs from behind existing cover (a sedge tuft, a boulder, and a low bedrock ledge). By approaching in a crawl from about 4 m away (behind this cover), he was able to achieve a viewing distance <1 m from the frogs. Observations were made continuously over 4 h except for a brief (about 10 min) interval when the 3 frogs from the 1st set of observations were captured and measured. By taking notes on his arm, CJR was able to maintain a more prone position and thus further minimize movements. Once the observer was positioned for viewing, his minor movements did not seem to disturb frogs; frogs swam toward CJR, surfacing repeatedly, some seconds after his assuming a viewing position. While CJR was in this observation position, several male frogs emerged from the water and took up positions 0.4 to 1.5 m from him, seemingly without regard for his presence. Immediately following the events reported below, the frogs were captured, measured, marked with PIT tags for individual recognition, and then released.

At 10:05 on 22 June 2004, CJR approached the breeding pool and saw 7 male *R. boylei* within 10 m of the pool's west margin, where portions of the surrounding bedrock were covered with shallow (<10 cm deep) water. The frogs were sitting in shallow water, periodically surfacing and making short (<1 m) movements; several

males were calling sporadically. Calls generally consisted of a series (5 to 7 notes) of distinct, rubbery clucks, described elsewhere as "longer-duration, pulsed calls" or "croaks" (MacTague and Northen 1993). On the initial approach of CJR, about 4 of these emergent males hid under submerged cobbles; they slowly emerged again over the next half hour. At 10:10, an amplexic pair (male: 51.5 mm SVL, 11.5 g; female: 59.0 mm SVL, 15.7 g) swam out of the center of the breeding pool. The pair entered the shallow east margin of the pool, which contained a pile of cobbles adjacent to a 17-cm-high bedrock ledge. After swimming around the cobble pile for about a minute, the pair stopped at a cobble (100 mm long \times 75 mm wide \times 65 mm high). For the next 10 min, the female moved over the surface of this rock (target cobble) using her hands and forelegs, then scraped the rock surface with her hind feet. During the scraping process, the female generally remained in 1 position, with her forelegs either braced on an adjacent rock or encircling the target cobble, keeping her hind feet pressed up against the surface of the target cobble. Periodically, she changed position, stopped for <30 s, then resumed scraping. The entire surface of the cobble was treated in this way. During the entire procedure, the male retained his hold of the female but did not contribute to the scraping process. After scraping the 1st cobble, the female (still in amplexus) swam to another cobble (100 mm long \times 25 mm wide \times 85 mm high) about 30 cm away. The female then began scraping this 2nd cobble in a manner similar to the 1st. After 7 min of scraping, she took up a position with her head and front legs raised on a rock adjacent to the newly treated cobble. Her hind legs were on the treated cobble, in a standard resting position (hind limbs folded against and slightly under the sides of the body), except that her heels were spaced slightly farther apart than usual (with approximately 2 cm between them). After holding this position for <30 s, she began to deposit eggs. Eggs initially appeared as a dense black-and-white mosaic that slowly spread over the surface of the rock and ultimately flattened out into a mass approximately 20 mm in diameter and several millimeters high. Egg deposition took about 1.5 min. As the eggs were being laid, the male lowered his vent toward the eggs and held it there without moving. The pair re-

mained essentially immobile during egg-laying. Five minutes post-laying, the egg mass measured 30 mm \times 40 mm \times 15 mm; approximately 20 min later, it had increased over an order of magnitude in volume (to 85 mm \times 65 mm \times 54 mm).

At 10:55, a 2nd amplexic pair (male: 53.0 mm SVL, 12.8 g; female: 74.4 mm SVL, 35.5 g) was observed approaching the oviposition site. The female of this pair immediately began visiting different rocks (mostly smooth, round cobbles). She swam up to and over the rocks, lowering her snout to the rock surface, and/or backing over them, with her palms flat on the rock. She then "walked" backward in this position over the rock's surface. Occasionally, she would back up onto or against a rock, resulting in contact with her rump or abdomen. Once in this position, she would attempt to grasp the rock with her outstretched hind legs. Prior to beginning actual scraping, this female thoroughly patted the rock with the soles and backs of her feet.

Over the next 3 h, this female examined over 20 rocks and engaged in the scraping of 14 separate objects. Twelve scraping episodes were made on smooth cobbles between 5 and 20 cm in diameter, and 2 were on the vertical surface of a 17-cm-high, rough-surfaced bedrock ledge. Scraping episodes lasted from 30 s to >10 min. The pair surfaced to gulp air no more than 7 times, averaging about 30 min submerged between gulps. When surfacing, they rapidly swam to the top, gulped air, and then swam quickly back down to a cobble. If disturbed by other frogs, they briefly hid under a cobble or an egg mass before the female resumed scraping. Some locations were visited more frequently than others; the pair sat under 1 previously deposited egg mass 7 times and cleaned the rock to which it was attached on 4 separate occasions. Occasionally, the female scraped a rock using both her front and hind feet, rubbing her front feet across the surface of the rock in an outward (medial to lateral) motion. All cobbles scraped by the female were smooth to the touch. Subsequent to capture of the frogs, 5 of the scraped cobbles were qualitatively compared to adjacent, unscraped rocks, and felt less slippery. Twice, the female scraped the bedrock shelf (which was considerably rougher to the touch than the cobbles) but did not scrape it for long (<2 min) before abandoning it for a new rock. Between scraping

episodes, the female swam around for a few seconds, then sat motionless for 4 to >60 sec before moving again. In this manner, the pair repeatedly covered an approximately 3-m² area during the 3 h of observation.

Both females used 3 distinct behaviors when scraping rocks: using the whole foot, using only the heel, and toe fluttering. Each behavior is briefly described.

Whole Foot Scraping.—In this behavior, the frog pushed the sole of its hind foot against a rock, and with a leg-extending motion, thrust its foot against the rock so that its foot slid back against the rock, with the distal edge of the foot being the last part to scrape the rock. When performing this motion, both females alternated use of 1 foot most of the time; infrequently, they used both feet simultaneously. Whole foot scraping was the predominant scraping behavior used by both frogs. It encompassed more than half of the total time spent scraping and was used on all rocks scraped.

Heel Scraping.—Here, only the heel of the hind foot came in contact with the rock. Otherwise, the behavior was similar to whole foot scraping: the frog would push its heel back against the rock, with its toes held up and away from the surface of the rock. It comprised <10% of the total time spent scraping and was not used until after at least half of the cobble had been covered using whole foot scraping.

Toe Fluttering.—In this behavior, the frog placed the heel of its foot firmly against the cobble, with its toes extended outward. The frog then flexed its toes, which all moved together in a fanlike motion, as with diving fins. In this way, the frog would fan its toes back and forth against the surface of the rock at a rate of 1 to 4 times/s. Both females used this behavior, but the 2nd female employed it more extensively and on several rocks. This behavior was never observed until after the rock surface had been scraped using 1 of the other 2 methods.

The substrate manipulation that we observed female *R. boylei* perform occurred during amplexus, preceded oviposition, and appeared to make rock substrates less slippery. This supports the hypothesis of Wheeler and others (2003) that the substrate was being prepared for egg mass deposition. Our observations also reveal greater complexity in substrate manipulation behavior than previously noted, of which 3 aspects merit discussion. First, visita-

tion (and revisitation) of more than 1 rock surface suggests that female *R. boylei* exercise selection in their choice of oviposition sites. Wheeler and others (2003) did not observe female *R. boylei* manipulating more than 1 rock or revisiting rocks, but variation in the availability of suitable oviposition sites may influence visitation patterns. Second, most rock surfaces scraped were relatively smooth, and less scraping was performed on rougher surfaces, implying that surfaces which are already smoother may be selected. From 2000 to 2004, 78% of egg masses (n = 119) observed at this site were deposited on smooth-surfaced rocks (unpubl. data). Third, the amount of coarse material we saw frogs scrape from rocks was small; the only obvious change detected in rock surfaces after scraping was that they appeared less slippery to the touch than rocks that had not been scraped. Stream surfaces exposed to light usually possess a surface "aufwuchs" algal film (Hynes 1970). In side pools with reduced flow, the aufwuchs tends to be dominated by green and blue-green algae and diatoms that have mucous or slime sheaths (Kupferberg 1996b), making rock surfaces slippery. We anticipate that removal of this film would increase egg mass adhesion as Wheeler and others (2003) suggest.

The substrate preparation (and presumably site assessment) behavior of *R. boylei* described here is 1 of a relatively large category of oviposition site modification behaviors in which many anurans engage. Significant effort has been devoted to describing site preparation behaviors that markedly modify the local environment for rearing embryos (for example, *Hyla rosenbergi*, Kluge 1981; *Chiromantis xerampelina*, Seymour and Loveridge 1994); the product of such behavior is typically labeled a "nest". The behavior of *R. boylei* described here is subtler because substrate preparation modifies the oviposition environment in a less obvious way. However, this behavior may be necessary to ensure egg mass adhesion to the oviposition surface. Better understanding of this behavior is important not only in its own right, but also because many aquatic-ovipositing anurans utilize some kind of oviposition brace to which to attach their egg masses. Such braces are vulnerable to algal and fungal colonization that could reduce egg jelly adhesion. Thus, heretofore unrecognized substrate preparation

behaviors may exist among anurans that deposit eggs on aquatic braces.

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