MOVEMENT, HABITAT, AND HOME RANGE OF INTRODUCED BULLFROGS (*LITHOBATES CATESBEIANUS*) ON MAD RIVER GRAVEL PONDS (HUMBOLDT CO., CA, USA), WITH IMPLICATIONS FOR HYDRO-MODIFICATION AS A METHOD OF MANAGEMENT

By

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ABSTRACT

MOVEMENT, HABITAT, AND HOME RANGE OF INTRODUCED BULLFROGS (*LITHOBATES CATESBEIANUS*) ON MAD RIVER GRAVEL PONDS (HUMBOLDT CO., CA, USA), WITH IMPLICATIONS FOR HYDRO-MODIFICATION AS A METHOD OF MANAGEMENT

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American Bullfrogs are a non-native, invasive species in California (USA), where they are known to have deleterious effects on many native species. Carnivorous adults prey on native amphibians and fish, while herbivorous tadpoles outcompete native tadpoles for algal food resources. Bullfrogs have been successful at colonizing old tailing ponds and other pools left over from mining activities, and these relict pools are common on many rivers in California. Information on the dispersal capabilities of Bullfrogs could help predict range expansions and inform management decisions. Unfortunately, this information is lacking from both their native and invaded range. From May to August of 2015, I used radio telemetry to track 29 Bullfrogs located in two gravel extraction sites (164 m apart) on the lower Mad River in western Humboldt County, CA. Four frogs (14%) switched between the two ponds over the three-month tracking period. I did not observe any frogs using the river channel or nearby seasonal wetlands. The mean home range size was 1600 square meters and did not differ by sex or age class. As a removal effort, both ponds were partially filled with gravel in September 2015 under the direction of the California Department of Fish and Wildlife (CDFW). In the following year, populations of Bullfrogs did not return to the survey area, even when the hydro-modified sites contained water, or when off-channel pools were present in the vicinity. Based on the timing of breeding and metamorphosis, as well as the lack of summer movements observed in this study,

pond filling may be most effective as an eradication tool between the culmination of egg laying and the end of metamorphosis.

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INTRODUCTION

The American Bullfrog (*Lithobates catesbeianus*; hereafter Bullfrog) is an invasive species in the western United States and 40 other countries around the world. It has been named one of the International Union for Conservation of Nature's (IUCN)100 worst invaders because of its ability to quickly outcompete native anurans, prey on fish, and carry the deadly amphibian disease, chytridiomycosis (Global Invasive Species Database, 2005). Bullfrogs, which are native to the United States east of the Rocky Mountains, were first introduced to California in 1914 and have since spread throughout the state (Moyle, 1973). Although Bullfrogs are frequently present in habitats that have been affected by human disturbance, they have also been found in otherwise pristine habitats around California (Kupferberg, 1997).

Introduced Bullfrogs have many negative effects on native fauna (Snow & Witmer, 2010). Bullfrogs have displaced native aquatic and amphibious vertebrates by a variety of mechanisms. In California, Bullfrog tadpoles decreased the survivorship and growth rates of tadpoles of Foothill Yellow-legged Frogs (*Rana boylii*, California Species of Special Concern) and Pacific Chorus Frogs (*Pseudacris regilla*) by limiting availability of benthic algae, their food source (Kupferberg, 1997). Another native species, the federally threatened California Red-legged Frog (*Rana draytonii*) is negatively associated with Bullfrogs, which are gape-limited predators and prey on Red-legged Frog tadpoles and juveniles (Doubledee et al., 2003; Moyle, 1973). Furthermore, federally endangered Coho Salmon (*Oncorhynchus kisutch*) smolts have been found in the stomach of Bullfrogs (Garwood et al., 2010). Bullfrogs are also considered a reservoir species for chytridiomycosis (Eskew et al., 2015), the disease responsible for frog population declines around the world (Skerratt et al., 2007). Bullfrogs carry the fungus

(*Batrachochytrium dendrobatidis*) that causes the disease, but are rarely negatively affected by infection (Adams et al., 2017; Eskew et al., 2015).

Efforts to control the spread of any invasive frog species must consider the complex life cycles that are characteristic of most species. Specifically, population growth rate may be affected to varying degrees by vital rates at specific life stages. For instance, population size of adult Cane Toads (*Rhinella marina*) is most strongly influenced by adult survival, rather than juvenile and tadpole survival, or clutch size (Lampo & Leo, 1998). Conversely, many ranid frog populations are most affected by fluctuations in juvenile populations (Biek et al., 2002). Because of this sensitivity to changes in juvenile population size, ranid eradication efforts should target juveniles for removal (Govindarajulu et al., 2005).

Due to the importance of targeting the correct life stage for removal, a good understanding of Bullfrog phenology – such as the timing of breeding, egg laying and metamorphosis – is necessary for effective population control. For Bullfrogs, this effort is complicated by the fact that phenology varies substantially over their range. Furthermore, little information on phenology has been gathered in areas where Bullfrog invasions have occurred (Bury & Whelan, 1985; Govindarajulu et al., 2006). Studies from their native range found that most females are ready to reproduce when they reach 128 mm snout-vent length (SVL), or two to four years after metamorphosis (Willis et al., 1956). Males mature earlier than females at approximately 100 mm SVL, or one to two years after metamorphosis (Howard, 1978a). Breeding can occur from early spring to mid fall depending on climate. Breeding adults must find an appropriate oviposition site where eggs will be safe from predators and experience proper hatching temperatures (Howard, 1978b). Larvae are aquatic and require warm water and algal food sources for development (Skelly et al., 2002). Most commonly, Bullfrog larvae take up to two years to metamorphose into juveniles, so a permanent water source is nearly always a requirement for Bullfrog success (D'Amore et al., 2010). Juvenile frogs are fully metamorphosed individuals less than 75 mm SVL that are not yet reproductive. Metamorphosed individuals that are between 75 mm and breeding size may be considered subadults, although the limited research on Bullfrog reproductive biology makes it unclear whether these individuals are reproductive if they are also showing secondary sex characteristics (large tympanum and thumb pads on males). Although permanent lentic water is not a common natural feature of northern California's rivers, a variety of mining activities can lead to the creation of permanent pools in river systems. These pools, and altered flow regimes due to river damming, have created large areas of potential Bullfrog habitat (Fuller et al., 2010; Doubledee et al., 2003).

Although understanding dispersal patterns of invasive species has clear implications for managing them, this information is largely lacking for Bullfrogs (Peterson et al., 2013; Adams & Pearl, 2007; Phillips et al., 2006). In studies of adult Bullfrog movements, the majority of frogs rarely moved farther than the shoreline of the water body at which they were captured (Willis et al., 1956; Currie & Bellis, 1969; Roninger, 2008, Stinner et al., 1994). However, these studies also observed individuals moving up to 1.2 km, though the factors that led to these long distance movements are unknown. The limited research available suggests that female Bullfrogs may move farther distances than males (Louette et al., 2014; Currie & Bellis, 1969; Berroneau et al., 2007). Even less information exists on how age affects dispersal. Willis et al. (1956) observed Bullfrog metamorphs away from ponds (distances not specified) and hypothesized that juveniles make up the majority of dispersing Bullfrogs, as they do in other ranid frog species, but this idea has never been tested (Dole, 1971; Martof, 1953). If juvenile Bullfrogs are the main dispersers, it is also important to determine when this dispersal takes place, to inform the timing of population control at a specific location.

Although targeting the juvenile life stage can increase eradication success, directly targeting individual Bullfrogs takes significant time and effort; consequently, there is interest in utilizing habitat modifications as a control measure (Adams & Pearl, 2007). Modifying habitats can reduce overlap between invasive and native species, and discourage invasive species from colonizing new areas, or force them out of habitats that were once suitable. For instance, models have shown that California Red-legged Frogs are able to coexist with Bullfrogs in ponds associated with rivers when those river systems flood at least every five years. Consequently, returning rivers to their natural hydrology to increase flood frequency could diminish Bullfrog populations. These floods reduce Bullfrog populations but do not harm California Red-legged Frogs, which are more able to utilize upland habitats (Doubledee et al., 2003). Dammed rivers and altered flow regimes have been associated with successful populations of invasive species and loss of biodiversity in floodplains (D’Amore et al., 2010; Rahel, 2002). Altered flow regimes due to dams can decrease the frequency of winter peak flows but increase summer base flows (Graf, 2006; Magilligan & Nislow, 2005). Decreased peak flows allow Bullfrogs to overwinter on rivers while increased summer flows may maintain permanent breeding ponds. On the Trinity River in northern California, Bullfrogs frequently use tailing ponds (pools left over from mining activities) as breeding sites (Fuller et al., 2010). Tailing ponds differ from active side channels in that they are deep and have a permanent hydroperiod. Restoring rivers to their natural hydrology and eliminating constructed pools used by Bullfrogs could discourage Bullfrogs and benefit native amphibians (Doubledee et al., 2003; Fuller et al., 2010). Effective plans for habitat modifications that aid in Bullfrog control require detailed data on habitat use and movement that are currently lacking (Adams & Pearl, 2007; Marvier et al., 2004).

The Mad River, in northwestern California, is the site of multiple anthropogenic modifications. The largest of those, a hydroelectric dam, forms Ruth Reservoir about 60 km downstream from the headwaters. Additionally, the lower Mad River in Humboldt County is currently being mined for gravel, and populations of breeding Bullfrogs are becoming established (Humboldt Country Planning and Building Department, 2014). Leftover mining pools can also act as fish traps when salmonid fry are washed into the ponds during high flows and then become trapped and die when flows decrease in the summer. Although the California Department of Fish and Wildlife (CDFW) has placed restrictions on the depth of mining pits, they are sometimes dug too deep and become permanent lentic habitat (van Hattem, pers. comm., 2015). At this point, these pools may attract breeding populations of Bullfrogs. Because these deep ponds violate the gravel mining permit, CDFW may require that they be hydro-modified as part of an effort to reduce Bullfrog breeding habitat and fish trapping on the Mad River. Because the lower Mad River represents the western edge of the Bullfrog's range in Humboldt County, this area is especially important for population control to prevent breeding populations from reaching the coast. Little is known about the basic biology of Bullfrogs in Humboldt County -- whether they disperse, home range size, and breeding phenology. Consequently, I used radio-telemetry to monitor the summer movements of juvenile and young adult Bullfrogs in two gravel ponds on the Mad River to determine if there was evidence for dispersal from their natal ponds. I also investigated timing of breeding, oviposition, and metamorphosis in this population.

A couple months into my study, both ponds were filled with gravel, under direction from CDFW and other permitting agencies, in an effort to eradicate these Bullfrog populations. After the hydro-modification event, I continued to monitor the sites for Bullfrogs and native species to (1) determine if pond filling was an effective Bullfrog eradication tool and (2) see how hydro-modification affected native amphibians.

METHODS

Study Site

Two ponds were located on a gravel bar of the lower Mad River in Blue Lake, Humboldt County, CA (Figure 1). Both ponds were established during gravel mining activities: gravel pond 1 (GP1) was created in 2010 and gravel pond 2 (GP2) was created in 2012. After the completion of mining operations in the immediate area, these ponds naturally filled with river water during winter flooding; their permanent hydroperiod is maintained by groundwater. GP1 was the smaller of the two ponds (GP1 = 1,510 m^2, GP2 = 1,676 m^2) but contained more emergent and submergent vegetation than GP2 (616 m^2 emergent vegetation measured at GP1 compared to 203 m^2 at GP2; Figure 1). All pond measurements were obtained by marking the perimeters of the ponds and vegetated areas with a handheld GPS unit, then digitizing those areas in ArcMap version 10.2.2 (Environmental Systems Research Institute, Redlands, CA). Both ponds were long and narrow and were oriented with their lengths running southeast to the river channel. Past satellite images and the presence of river species in the ponds provided evidence that the ponds were connected to the main channel of the Mad River during winter high flows. A nearby gravel pond (GP0) had been created in 1995, then hydro-modified in 2012, prior the start of this research. Other than GP0, the ponds nearest to GP1 and GP2 were a seasonal pond (SP) located across the river, and a complex of gravel mining ponds (GDP) located upstream of the study site on land owned by Green Diamond Resource Company (Figure 2).

During the first week of September 2015, GP1 and GP2 were filled with gravel by the permitted gravel mining company, as required by CDFW as part of an effort to reduce Bullfrog populations and prevent the fish trapping that was occurring in the ponds.

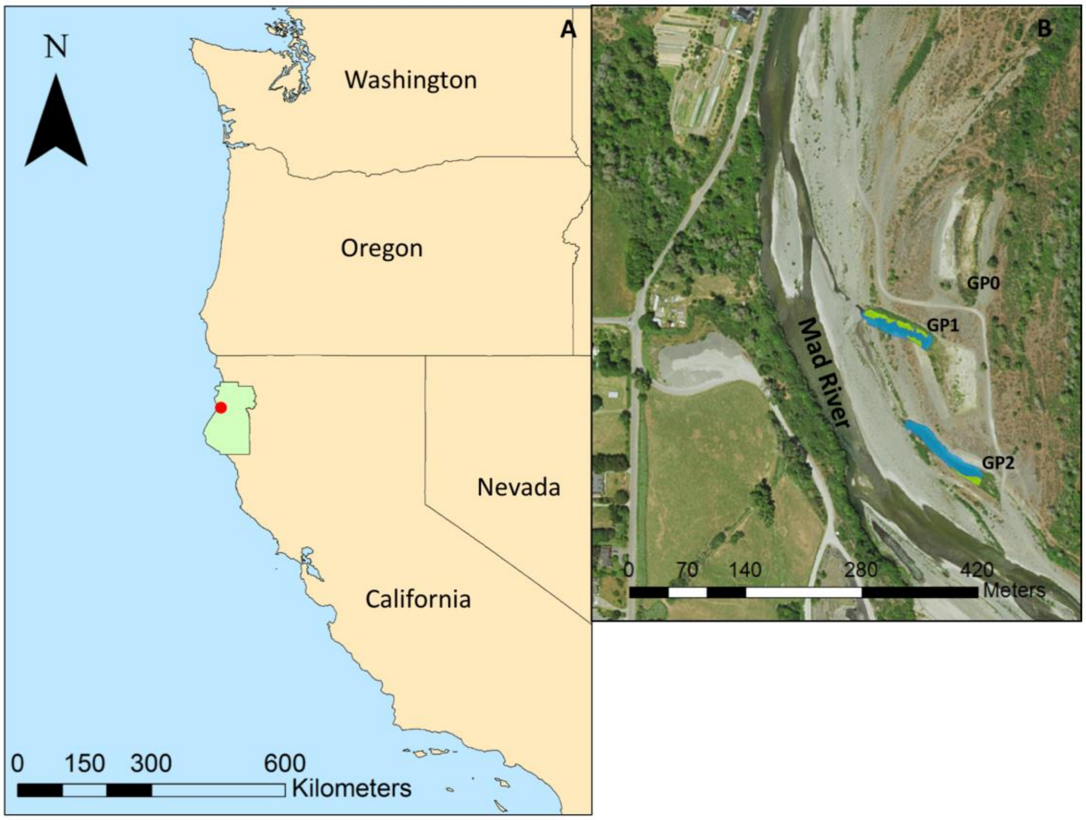

Figure 1. A) Location of study site (red dot) in Blue Lake, Humboldt County (shown in green), California. B) Aerial photo showing location of field sites on the lower Mad River. All Bullfrogs were monitored at gravel ponds 1 and 2 (GP1 & GP2). Digitized outlines of ponds are shown: blue represents open water, and light green indicates emergent vegetation. GP0 was a gravel pond that was subsequently filled with gravel in 2012; prior to hydro-modification, it contained water and Bullfrogs. The extent of GP0 is visible in the image as a beige oval surrounded by vegetation.

Figure 2 . Location of other ponds in the nearby landscape where no radio tracked Bullfrogs were observed. Ponds and pond complexes are indicated in red boxes. GP1 = gravel pond , GP2 = gravel pond , SP = seasonal pond, GDP =Green Diamond Resource Company gravel ponds (individual ponds outlined in red). For digitized ponds, blue represents open water, and light green indicates emergent vegetation. The downstream direction is at the north end of this map.

Telemetry

I tagged 29 Bullfrogs with radio transmitters (model SOPR-2070, Wildlife Materials, Murphysboro, IL) between May 29 and June 30, 2015. Each transmitter weighed 2.9 grams and had an expected battery life of 130 days, though five batteries (17.2%) failed after 57 to 85 days. To ensure that no frog would be tagged with a transmitter weighing more than 10% of its body mass, I only tagged frogs that weighed at least 29g at the time of capture (Richards et al., 1994). Because I was interested in the movement patterns of juveniles, I primarily attempted to tag frogs that measured less than 75mm SVL (Willis et al., 1956); however, because I was unable to capture enough juvenile frogs that were less than 29 g I ultimately tagged 10 frogs (five males, five females) that measured over 75 mm SVL, in addition to 19 juveniles. Although it was unknown whether these frogs were sexually mature, their larger size indicated they had metamorphosed the previous year. Adults were sexed based on the size of the tympanum, with males having a tympanum larger than the size of the eye (Stebbins, 2003). Tracking continued for three months, until the ponds were filled in on September 3, 2015.

I caught frogs at night, by net or hand with the aid of a 130 lumen headlamp. Transmitters were attached to frogs using a belt made out of 0.1 mm elastomer thread. Polyolefin heat shrink tubing (Gardner Bender, Menomonee Falls, WI) was used to cover the knot to avoid abrading the skin. The belt was slipped over the frogs' hind legs onto the waist and fit was checked by looking for areas of wrinkled skin and by attempting to gently pull the radio back down over the legs (Groff et al., 2015). After being tagged, frogs were re-released into their pond of capture. All tagged frogs were also uniquely marked with visual implant elastomer (VIE) so they could be identified if the belt was lost (Pham et al., 2007).

Each frog was located once a day, six days a week using a Telonics TR-4 receiver and antenna (Telonics, Inc., Mesa, AZ). Visual confirmations of location were not usually possible, so I marked a frog's location only if I was getting the strongest signal from the receiver without the antenna attached. Without the antenna, I could get a strong signal in an approximately one square meter area. Locations were marked using a handheld GPS, habitat was recorded (open water, emergent vegetation, or land), and a note was made if the frog had moved from its original pond.

Mark-Recapture

In addition to the 29 frogs that were fitted with radio transmitters, I marked 102 frogs with VIE from June through early August 2015. Frogs were given a unique combination of colored marks under the skin of the front and hind feet so that individuals could be recaptured and uniquely identified. There are no size restrictions for marking with VIE so I marked frogs of all ages and sexes (Pham et al., 2007). Capture/recapture attempts were made one night per week at both ponds in an attempt to detect movement between the ponds. I used a spotlight to locate frogs, then caught them by hand or net.

Movement Extent, Home Range, and Habitat Use

I calculated movement distances and home range size for all radio tracked frogs. All location points were projected into UTM NAD83 Zone 10N (Universal Transverse Mercator North American Datum 1983). Distances in meters between location points (path lengths) were obtained using the Geospatial Modelling Environment, a program that allows for quantitative analysis of spatial data (Beyer, 2012). Kernel density home range analysis was performed using the adehabitatHR package in R (Calenge, 2006; R Core Team, 2015). The smoothing parameter (h-value) was chosen for each frog using the Least Squares Cross Validation (LSCV) method, which reduces bias in the 95% fixed kernel home range relative to when the reference bandwidth smoothing parameter (href) is used (Seaman et al., 1999; Watson et al., 2003). H-values converged for all frogs and ranged from 1.36 to 8.63 (Appendix A) and the 95% home range area was estimated in square meters (m^2). To account for inaccurate detections during a period of equipment malfunction (08/04/2015 – 08/18/2015), points taken during these days were not used in analysis. Frogs that had fewer than 30 location points were excluded from the analysis because the kernel density method overestimates the size of the home range when less than 30 points are used (Seaman et al., 1999). Home range sizes were compared between frogs of different sexes, life stages (sex/stage) and weight. The home range size data were not normally distributed in each sex-stage group, so a Kruskal-Wallace test was used to compare home range area for males, females and juveniles. Linear regression was used to determine if there was a relationship between SVL and home range area. To determine whether individual frogs were using the vegetated or open water habitats more frequently, I used a chi-square test for each frog to compare use versus availability of open water and emergent vegetation. I performed the same chi-square test using all in-pond location points to check whether the Bullfrog population overall was preferentially using certain habitat. I did not use the few points taken on the banks of the ponds because I was not able to quantify the available land area. For all statistical tests the relationship was considered significant at the alpha = 0.05 level.

Visual Encounter Surveys

From May 31 through August 23, 2015, I performed a visual encounter survey (VES) once a week at each pond by slowly walking the perimeter of the pond, counting all visible amphibians and identifying them to species and life stage. Because the number of visible frogs strongly depended on weather, I conducted VES on sunny, warm days, when the most frogs were basking at the water's surface. Bullfrog tadpoles older than 1 year (1+) were identified by their large size. I did not count the number of young-of-the-year tadpoles (YoY) but their presence was noted. I counted Bullfrog egg masses, which were identified by their large size and the fact that they float in a sheet on the surface of the water. Bullfrog egg masses can hatch in as little as three days from oviposition, so I included any new masses seen since the last VES in the egg mass count. New masses were marked with a nearby stick to avoid double counting. I plotted the number of adult, juvenile and 1+ tadpoles seen over time to determine when metamorphosis was taking place. To assess overall diversity in the ponds I also identified any other aquatic vertebrates using the ponds. Western Toad tadpoles were identified by their small size and uniform, black coloring. Pacific Chorus Frog tadpoles were distinguished from Northern Red-legged Frog tadpoles by the location of their eyes: the eyes of Pacific Chorus Frog tadpoles are located on the sides of the head, whereas eyes of Northern Red-legged Frog tadpoles are located more dorsally (Stebbins, 2003).

Habitat Modification and Subsequent Monitoring

Pond filling was required by CDFW and then completed by a local gravel mining company; it was not a planned part of this research. During the first week of September 2015, GP1 and GP2 were filled with gravel and dirt using a bulldozer. Filling each pond took approximately four hours. During this time, three people, including myself, were on site to catch escaping Bullfrogs and rescue native species. All captured Bullfrogs were checked for VIE marks or radios, and then euthanized with MS-222 (Tricaine mesylate), as required by CDFW as a condition of my scientific collecting permit. In the week prior to pond filling, I used aquatic funnel traps to recapture as many radio tracked Bullfrogs as possible to recover the radios. Any captured Bullfrogs were checked for VIE marks, then euthanized. Just prior to pond filling there were 19 radio tracked frogs still located in the ponds (see Appendix A for frog fates). The day after the ponds were filled, I returned to determine how many frogs had been trapped and killed as a result of pond-filling activities. I concluded that frogs had been killed if I detected a clear radio signal from beneath the gravel. None of the radios that had early-failing batteries were detected after the filling so it is uncertain whether these frogs escaped or had been buried with their failing radios.

I returned to the sites between November 2015 and August 2016 to perform visual encounter surveys and note any changes in standing water levels and vegetation cover at the filled pond sites. I included GP0 in these searches because it was hydro-modified three years before GP1 and GP2 were filled. Vegetation had more time to regrow here, so it not only serves as a preview of what GP1 and GP2 may look like in a few years, but also may act as a refuge for native amphibians or Bullfrogs that escaped from the filled sites. I was unable to access the sites in December 2015 because of high flow conditions. After winter flow conditions lowered, I surveyed twice a month during the day and once a month at night, and recorded the presence of any amphibians, measured maximum depth in centimeters of standing water, and estimated coverage of vegetation re-growth. After standing water in the pond sites had completely dried, I surveyed once a month during the day.

RESULTS

Movement Extent

All 30 radio-tagged frogs (GP1: 12 juveniles, 5 females, 3 males; GP2: 6 juveniles, 1 female, 3 males) were most frequently located in the pond, or on the bank less than a meter from the water's edge. The average distance between two successive location points (excluding between-pond movements) was 14.98 $\pm$ 12.58 m and the majority (96%) of all frog movements were less than 50 m (Figure 3). The maximum movement distance was 194 m and represented the movement of a juvenile frog between the two ponds. Four of thirty (13%) radio tracked frogs moved from one pond to the other over the tracking season; three of these between-pond movements were from GP2 to GP1. The frogs that moved between ponds, and thus had the highest maximum movement distances were not the frogs with the highest mean movements (Figure 4). Because of equipment malfunctions, the date of movement is only certain for two of these frogs, while there is a two-week window when the remaining two frogs could have moved. I never recaptured a frog marked with VIE at a different pond than where it had been originally tagged.

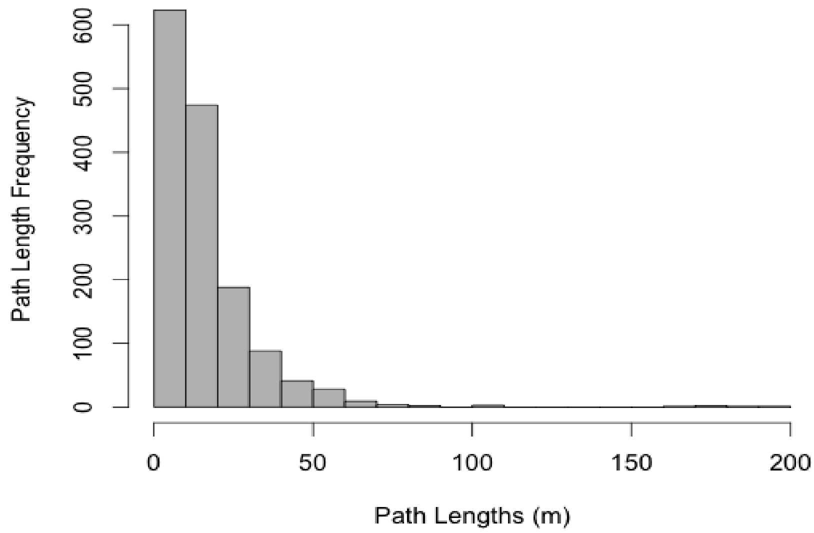

Figure 3. Histogram of Bullfrog path lengths (the straightline distance between two consecutive location points in 10 m increments). N = 1,417 paths.

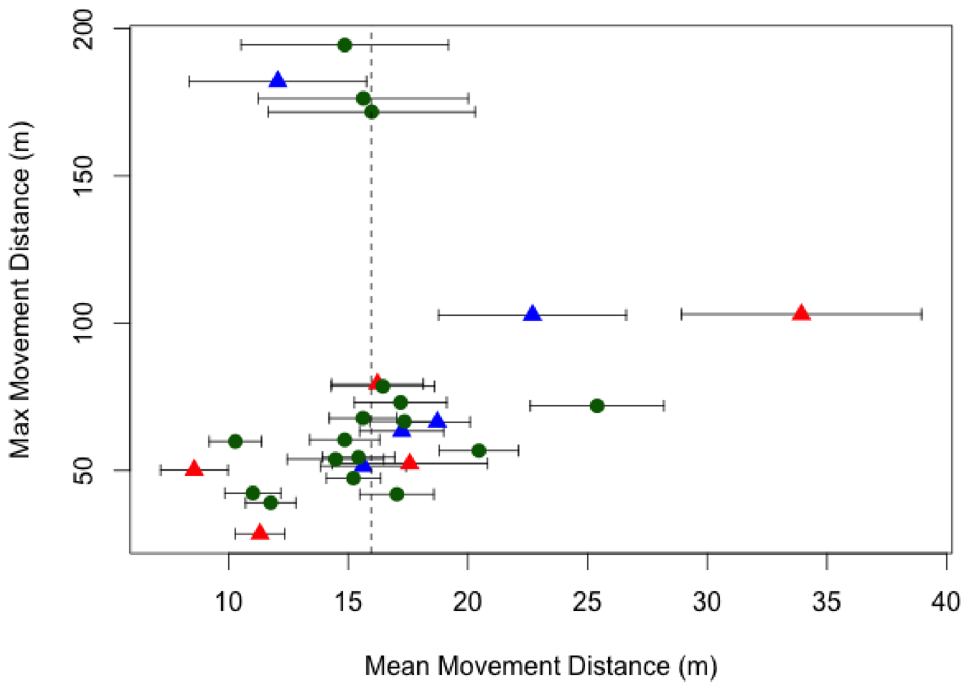

Figure 4. Comparison between mean and maximum Bullfrog path lengths in meters. Red triangles = adult females, blue triangles = adult males, green circles = juveniles. Error bars represent standard error around the mean. Dotted line shows the mean movement distance for all frogs.

Home Range and Habitat Use

The mean 95% kernel density home range area for all 29 radio tracked frogs was 1610 $\pm$ 970 m^2; all home ranges were centered on the ponds. There was a marginally significant relationship between frog SVL and home range size (Figure 5A; $p = 0.10$, $R^2 = 0.10$, df = 25). There was no significant difference in home range sizes based on sex or life stage (Figure 5B; $p = 0.15$, Kruskal-Wallace $X^2 = 3.84$, df = 2). However, juvenile frogs tended to have a smaller home range than adults of either sex, and adult males tended to have smaller ranges than adult females. Overall, Bullfrogs did not preferentially use open water or emergent vegetation habitat, although eight individual frogs had strong, significant preferences for emergent vegetation (Figure 6, Tables 1 & 2).

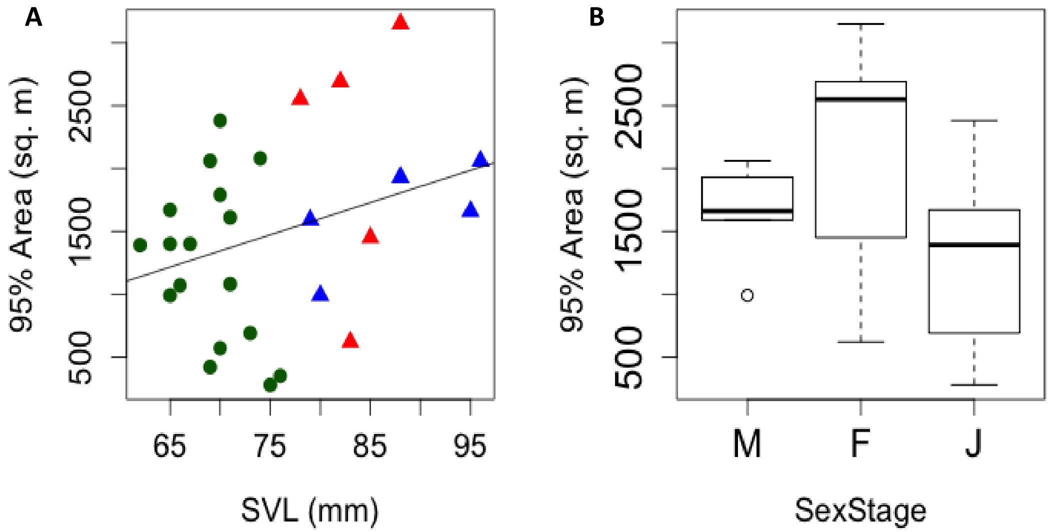

Figure 5. Comparisons of home range area to Bullfrog size and sex/stage. A) Comparison between home range area and frog snout-vent length (SVL) with linear regression line ($p = 0.10$, $R^2 = 0.10$, df = 25). Green circles represent juveniles, red triangles represent adult females and blue triangles represent adult males. B) 95% kernel density home range areas (m^2) for Bullfrogs of different sexes and life stages. M = males (n = 5), F = females (n = 5), J = juveniles (n = 17). No significant differences exist between any groups

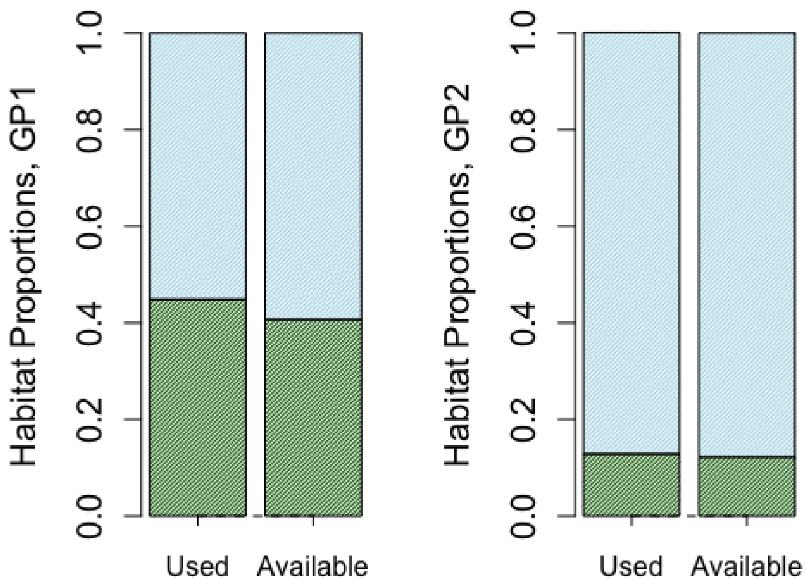

Figure 6. Use versus availability for open water and emergent vegetation for frogs in GP1 and GP2 using one or both ponds. Blue = open water, green = emergent vegetation.

Table 1. Chi-square test statistics for use vs. availability comparison for Bullfrogs that used one or both ponds over the summer of 2015. In all tests DF = 1.

	X^2	P
GP1	0.007	1
GP2	0.0003	1
Both	0.008	1

Table 2. Chi-square results for individual Bullfrogs showing differing preference for emergent vegetation habitat. In p-value column * indicates a frog with a strong preference for vegetated habitat.

Frog #	X^2	P
569	23.75	0.000001*
248	15.06	0.0001*
208	14.56	0.0001*
489	14.44	0.0001*
91	6.56	0.01*
409	5.35	0.02*
11	4.80	0.028*
371	3.86	0.049*
171	3.35	0.066
431	3.15	0.076
151	3.12	0.076
231	1.73	0.19
549	1.67	0.19
389	1.67	0.19
449	1.11	0.29
111	1.05	0.31
329	0.89	0.34
347	0.86	0.35
191	0.76	0.38
49	0.42	0.52
71	0.42	0.52
291	0.41	0.59
309	0.41	0.59
271	0.31	0.57
131	0.28	0.59
511	0.13	0.72
31	0.099	0.75
469	0.002	0.97
912	0.002	0.97
531	0.000005	0.99

Phenology and Visual Encounter Surveys

Male Bullfrogs made breeding calls throughout the summer at both ponds. Breeding call frequency (calls/hour) peaked in late July in GP1, whereas calling rates were low throughout the summer in GP2 (Figure 7). Calling rates were not related to the number of egg masses or YoY tadpoles observed; both of which were much higher in GP2 (Figure 7). The last egg mass of the season was observed mid-August in GP2 (Figure 7).

Counts of Bullfrogs at all life stages in the ponds varied throughout the summer. Numbers of juveniles in GP1 steadily increased for the majority of the summer and peaked on the July 31st survey, with 158 individuals counted (Figure 8). Counts of adults in this pond ranged from 4 to 33 and peaked between June 22 and July 5. The increase in number of adults detected in the early summer may have been more related to an increase in frog activity levels as the weather warmed than to an actual increase in frogs present. There was an overall increase in the number of 1+ tadpoles between the first survey in which they were included (June 7th) and June 22nd. After this date there was a sharp decline in the number 1+ tadpole as most tadpoles completed metamorphosis. After the June 22nd survey, all 1+ tadpoles observed in the ponds were at various stages of metamorphosis and were exhibiting presence of front and hind limbs of various sizes, changing mouth morphology, and shortening tails. After the July 16th survey, I did not observe any more 1+ tadpoles, though at the end of August I caught two in aquatic funnel traps. These 1+ tadpoles were larger than the 1+ tadpoles that had been observed earlier in the summer and they exhibited no signs of metamorphosis (i.e., no limbs present, tadpole mouths and full tails). GP2 had lower Bullfrog populations overall and no 1+ tadpoles, indicating that breeding had not occurred in this pond the previous year, or that no tadpoles had survived the winter. However, after the July 16th survey juveniles were observed in the pond and increased in numbers through the end of the summer with an ending count of 25 juveniles (Figure 8). In GP2, there were low counts of adults throughout the summer, ranging from one to nine individuals.

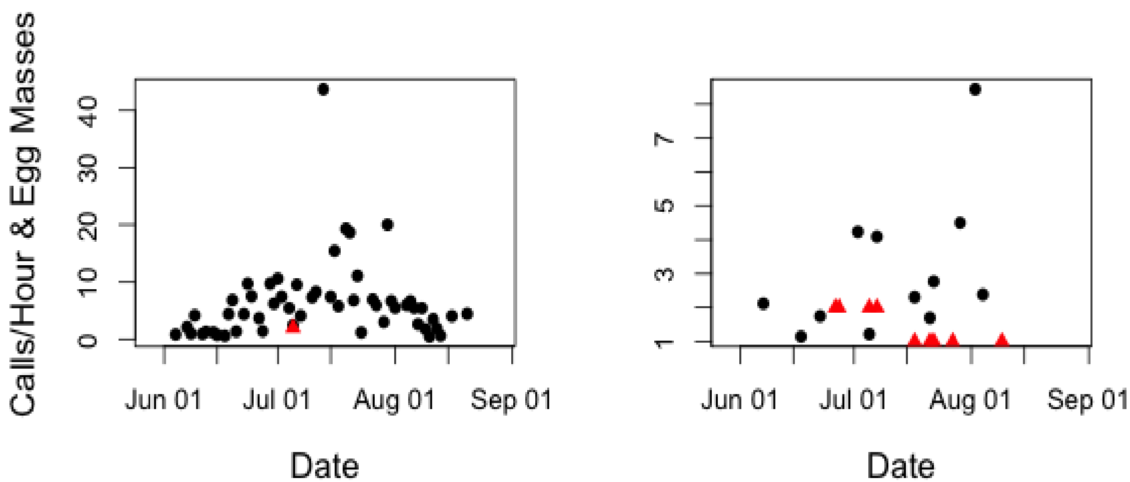

Figure 7. Breeding call frequency and number of new egg masses in GP1 (left plot) and GP2 (right plot) over the summer of 2015. Black circles represent calls per hour and red triangles represent number of new egg masses. Note that the y-axis has different scales for GP1 and GP2

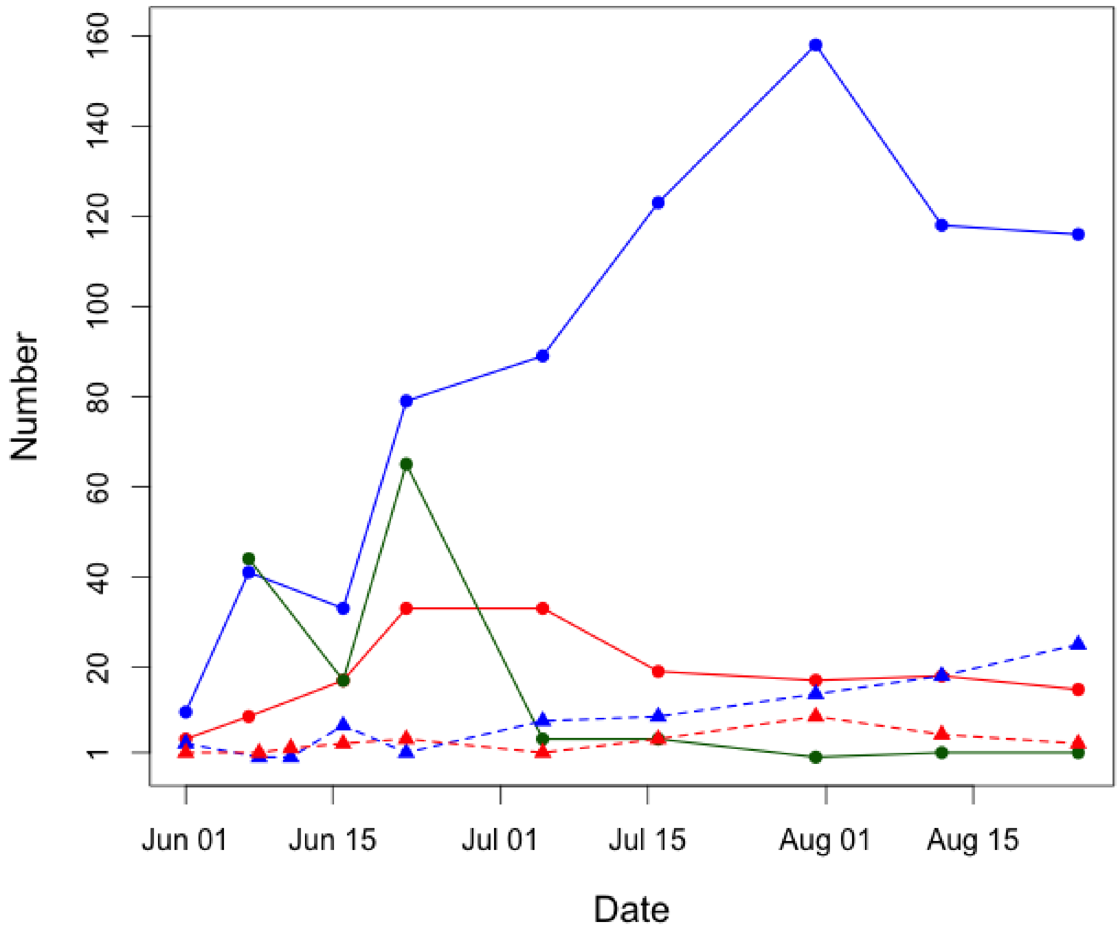

Figure 8. Numbers of Bullfrogs observed on visual encounter surveys from June 1st, 2015 to August 24th, 2015. Frogs are separated by pond and life stage. Solid blue line = GP1 juveniles, solid red line = GP1 adults, solid green line = GP1 1+ tadpoles (older than one year), dotted blue line = GP2 juveniles, dotted red line = GP2 adults. There were no 1+ tadpoles in GP2.

Prior to hydro-modification, both ponds had populations of Foothill Yellow-legged frogs, Northern Red-legged frogs, Boreal Toads (*Anaxyrus boreas*), Pacific Chorus Frogs, and Rough-skinned Newts (*Taricha granulosa*). Based on the presence of tadpoles and/or larvae, breeding was confirmed for Pacific Chorus Frogs, Northern Red-legged Frogs, Boreal Toads and Rough-skinned Newts. The ponds also contained Steelhead (*Oncorhynchus mykiss*), Lamprey ammocetes (*Entosphenus sp*.), Sacramento Suckers (*Catostomus sp.*), Stickleback (*Gasterosteus aculeatus*), Mosquitofish (*Gambusia affinis*), Crayfish (*Procambarus sp*.) and freshwater mussels (multiple genera possible) (Appendix B).

Habitat Modification and Subsequent Monitoring

In terms of immediate population control, between 76 and 100% of radio tracked frogs were buried and killed during the pond filling. Fates of other frogs are detailed in Appendix A. The day prior to hydro-modification, I located 16 radio tracked frogs in GP1 and GP2, but was unable to detect the five frogs with failing radios. Consequently, somewhere between 16 and 21 radio tracked frogs were still present in the ponds on the day that the ponds were filled, but I am uncertain of the exact number of frogs because of the five radio batteries that failed prior to the end of the study. The day after pond filling, I once again detected 16 frogs in the area of the old ponds (now filled with mud and gravel). I was still unable to detect the frogs with failing radios, so the actual percentage of buried frogs depends on whether any of these frogs escaped. Based on the limited movement seen before and during the hydro-modification it is unlikely that these frogs with failing batteries had either left the pond before modification or escaped during modification.

In an attempt to create seasonal wetlands that would accumulate water in the winter, neither pond was filled with dirt and gravel to the level of the river bar. However, high flows in late January 2016 completely filled GP2 with a mixture of fine to cobble-sized sediment; as a result, no water accumulated in this area and no vegetation regrowth occurred at the GP2 site. After the hydro-modification, the GP1 site contained mostly fine sediment. The water level at this pond site reached a maximum depth of 23 cm of standing water by the end of the winter high flows, though water levels may have been higher during the highest flows when I was not able to access the site. There was no emergent vegetation to provide wetland habitat in GP1 during the winter of 2015-2016. Although many of the cattails were buried during the hydromodification there was some regrowth of cattails and willows along the old pond margins in the late spring and early summer. GP0 was the site with the most plant species, the greatest plant growth, and the most water accumulation. Accumulated water had dried by April in GP1 and by June in GP0 (Table 3).

In the year after GP1 and GP2 were hydro-modified, I detected amphibians only at the GP0 site. During visual encounter surveys I observed adult Pacific Chorus Frogs, juvenile and adult Foothill Yellow-Legged Frogs, a single juvenile Bullfrog, Pacific Chorus Frog tadpoles, and a single Northern Red-legged Frog tadpole (no egg masses detected). The GP0 pond site (133 m from GP1, 158 m from GP2) contained more water and more emergent vegetation than either GP1 or GP2. The nearby seasonal pond was washed out during winter high flows, so I did not survey there.

During the late spring and early summer of 2016, I identified the plants growing in GP0 with a dichotomous key and the help of a botanist. Because of its proximity to GP1 and GP2, and the fact that it has had three more years for plant regrowth, the plants growing there may be a good predictor of the type and amount of vegetation to be expected in GP1 in the future – as long as that site is not filled in by high river flows. A total of 14 plants were identified to genus, 11 of which were also identified to species. Forty-three percent of plants are native to California, 36% are introduced and 21% are genera that have both native and introduced members and could not be keyed to species (Appendix C).

Table 3. Water accumulation (depth and coverage area) and vegetation regrowth in three hydro-modified pond sites (Figure 1B) on the Mad River (Humboldt Co., CA). Veg. growth refers to new vegetation growth in the winter of 2015 through the summer of 2016 and did not include coverage of dead vegetation from previous years. After GP2 was filled with cobble by high flows there was no longer area for water to accumulate or vegetation to grow (indicated by dashes).

	GP0		**GP1**		**GP2**	
	Water Depth	Veg. Growth	Water Depth	Veg. Growth	Water Depth	Veg. Growth
Nov	≤ 125cm throughout	No new veg.	≤ 10cm (puddles)	< 20 cattail stems	None	None
Dec	Flows too high to access site					
Jan	≤ 125cm throughout	Veg. emerging at pond margins	Level of river bar, connected to main channel	< 20 cattail stems	≤ 10cm	None
Feb	≤ 50cm throughout	Patchy veg. throughout	None	< 20 cattail stems	Filled in with cobble & sand	Filled in with cobble & sand
Mar	≤ 50cm throughout	Patchy veg. throughout	≤ 10cm (50% of pond area)	< 50 cattail stems	-	-
Apr	≤ 50cm on north & east edges	Patchy veg. throughout	None	< 100 cattail stems	-	-
May	≤ 30cm on north & east edges	Completely vegetated	None	< 100 cattail stems	-	-
June	None	Completely vegetated	None	< 100 cattail stems	-	-
July	None	Vegetation dying back	None	< 100 cattail stems	-	-
Aug	None	Vegetation dying back	None	< 100 cattail stems	-	-

DISCUSSION

Overview

Based on the summer movement behavior of Bullfrogs on the Mad River and the lack of Bullfrog detections post hydro-modification, this process appears to have been an effective method of Bullfrog control. Without prior radio-tracking and monitoring of breeding activity, the success of hydro-modification would have been unclear. The late summer timing of the filling meant that even if some frogs had escaped there was limited suitable habitat available, and since breeding had ended for the season there was little danger of gravid females reproducing in other locations. Because there was no observed summer dispersal, I am confident that frogs had not left the ponds before the modification took place, so hydro-modification not only eliminated Bullfrog habitat, but also the majority of the population.

Movement Extent, Home Range and Habitat Use

My results are consistent with those from other Bullfrog movement studies, which have reported short movements overall, occasionally punctuated by longer distances traveled (Appendix D). Of the six studies that examined Bullfrog movements, most reported that individual Bullfrogs stayed within their ponds of capture, and maximum out-of-pond movements ranged from 100 to 1,200 m (Currie & Bellis, 1969; Raney, 1940; Roninger, 2008; Stinner et al., 1994; Willis et al., 1956). The longest movement record comes from an individual in Klamath Falls, Oregon and represents a 1,200 m movement from a canal to an overwintering location in a nearby river floodplain (Roninger, 2008). Although the Klamath Falls study is most similar to mine in terms of climate and habitat, there are several differences that may explain Roninger's observation of movements up to six times the maximum distance reported in my study (194 m). Oregon Bullfrogs were captured in a canal system, not in ponds, and were tracked from September to November. These long distance movements could be explained by the rainy fall climate in the Pacific Northwest, which may be more conducive to frog movements, or by the fact that the canal was not a suitable overwintering location and Bullfrogs were forced to leave for the winter. Because the Bullfrogs I tracked were already living in ponds, not a canal or river, they may have been less likely to move from their winter location at the bottom of the ponds.

Four other Bullfrog movement studies occurred in summer months, over a similar time frame as my study (Berroneau et al., 2007; Currie & Bellis, 1969; Raney, 1940; Willis et al., 1956). Three of these studies took place in midwestern and eastern North America, where summers are warm and rainy, in contrast to the dry, temperate summers of northwestern California. These studies all noted that Bullfrogs were more frequently observed away from ponds on warm, rainy nights. However, during summer tracking in Missouri, only 8% of tagged frogs moved between ponds, and maximum movement distance was related to the distance between ponds (Willis et al., 1956). If long distance movement is stimulated by warm rainy conditions, then tracking would need to be done in the fall or winter to detect dispersal movements in coastal northern California. The only study to report Bullfrogs dispersing from ponds took place in southwestern France. These frogs left their hibernation ponds in the spring, as temperatures warmed and there was some rain, stayed in a nearby flooded area for a month, then returned to the pond for summer breeding (Berroneau et al., 2007). Although this shows that Bullfrogs may disperse from ponds in some situations, neither this particular dispersal event, nor longer movements seen in other studies, provide much information about the circumstances under which dispersal movements may occur.

Habitat availability and topography should be considered when examining the relative lack of movement seen in my study. Lack of suitable habitat in the landscape may have restricted movement. The next nearest ponds to GP1 and GP2 were the seasonal pond (SP) on the west bank of the river and the complex of several gravel mining ponds (GDP) located upstream on the east bank on Green Diamond Resource Company land. Populations of Bullfrogs were found in the Green Diamond gravel ponds in the late 1990s, but have not been observed there for several years (Diller, pers. comm., 2015). Since the summer of 2016, these ponds have become seasonal wetlands that dry in the summer, so they are no longer ideal Bullfrog breeding habitat, although Bullfrogs have occasionally been observed using seasonal ponds (Gahl et al., 2009). Although GP2 is closer to the seasonal pond than it is to GP1, no frogs that left GP2 traveled to the seasonal ponds (Appendix A). All movements out of the study ponds were between GP1 and GP2, which are permanent ponds on the same river bank. Movement distances may be more constrained by topography than distance. There is some evidence that Bullfrogs are more likely to move overland to nearby (< 1 km) wetlands than they are to use lotic water connections for movements between wetland sites (Peterson et al., 2013). However, Bullfrogs in southwestern France were observed crossing a river multiple times (Berroneau et al., 2007). River characteristics, such as low velocity and warm temperature, probably play a role in whether Bullfrogs are likely to cross flowing water. Another factor that may influence where and whether Bullfrogs disperse is the extent of pond vegetation. GP1 and GP2 were vegetated, permanent ponds, which Bullfrogs tend to prefer (Adams & Pearl, 2007; Fuller et al., 2010). As long as GP1 and GP2 could still support all resident Bullfrogs, there would have been little incentive for juveniles to travel 900 – 1100 m to the Green Diamond Ponds, or cross the Mad River to the nearby seasonal pond, especially because these seasonal ponds did not contain ideal Bullfrog habitat. It is possible that had Bullfrog populations at GP1 and GP2 increased further, more Bullfrogs would have dispersed to the less occupied GP2 or moved further across the landscape.

The other factor that may influence Bullfrog dispersal is seasonal weather patterns. Although summer is generally considered to be their active season, and is certainly their breeding season in northwestern California, out-of-pond movements seen in other studies are from regions where summers are rainy. By contrast, Humboldt County receives most of its rain in the fall and winter, leaving only a small window of time in the early fall when weather may be rainy and warm. I originally planned to track Bullfrogs in the summer months to capture the movements of the most recently metamorphosed juveniles, which Willis et al. (1956) hypothesized were the main dispersers. However, if long distance movements are more tied to rainy weather patterns than age, I likely missed these movements by not tracking frogs in the fall and winter.

Although only three radio tracked juveniles were observed moving between ponds, and no VIE-marked juveniles were ever recaptured in a different pond than the one in which they were marked, the total number of juveniles making between-pond movements must have been higher than I detected. No 1+ tadpoles were ever observed in GP2, but the presence of juvenile Bullfrogs in this pond throughout the summer (Figure 8) shows that some individuals moved from GP1 to GP2. The reason for the lack of 1+ tadpoles in GP2 is unknown, but may have been due either to no breeding in the previous year, or because the pond was washed out over the winter of 2014 and no tadpoles survived the flooding. The latter scenario would suggest that adults from GP1 had recolonized GP2 after winter flows lowered, but before I began my study.

All home ranges were clearly centered on GP1 and GP2, and within the ponds some Bullfrogs preferentially used habitat containing emergent vegetation. This underscores previous research that strongly ties Bullfrogs to vegetated, permanent lentic water and is consistent with past studies that most frequently located Bullfrogs on the banks of ponds in reeds, or in the shallow, vegetated water (Adams & Pearl, 2007; Fuller et al., 2010; Peterson et al., 2013; Raney, 1940; Willis et al., 1956). Some frogs had home range estimates larger than the area of the ponds. While frogs were occasionally located on the banks of the ponds, they were never located more than a meter from the water, suggesting that my home range estimates may be artificially inflated. This inflation may be related to the Least Squares Cross Validation (LSCV) method that was used to determine the smoothing parameter. Although the LSCV method is generally accepted as the most accurate way to estimate kernel density home ranges, it may still inflate the home range area when points are clustered in a small area, as they were for many of the Bullfrogs in my study (Gitzen et al., 2006; Seaman et al., 1999).

Comparing mean and maximum movement distances for individuals shows that the frogs making between-pond movements were not the frogs that made the longest movements within their original ponds. In fact, all four frogs that moved between ponds had mean in-pond movement distances within three meters of the overall mean movement distance. This indicates that an individual’s movement distance within a pond is not a good predictor of its overland movement capabilities. This is similar to the pattern seen in New York, where Bullfrogs that made the longest distance movements were not those that were actively moving within the pond (Raney, 1940).

Using Phenology and Environment to Inform Timing of Hydro-modification

Because Bullfrog phenology is so variable by region, understanding regional variation in life events should increase the efficacy of hydro-modification as a method for population control (Govindarajulu et al., 2006). Phenological information relevant to population control includes timing of breeding and metamorphosis, and whether dispersal is expected. To prevent adults from escaping a hydro-modified pond and then breeding in the same year, pond filling should occur after egg laying has finished for the season, so that all YoY and any remaining 1+ tadpoles are buried. When pond conditions are good, and Bullfrogs do not disperse, hydro-modification can be an effective method to reduce populations and eliminate habitat.

My study results suggest that hydro-modification in late summer was an effective tool for eliminating a large number of bullfrogs in the population. The low water level in and around the river at this time of year meant that even if some Bullfrogs escaped, they would have had very limited options for suitable fall habitat. Due to their highly aquatic nature and apparent lack of estivation, it is unlikely that Bullfrogs could survive out of water from late summer, when water levels are lowest, until seasonal ponds were filled during winter storms (Casper & Hendricks, 2005; Secor, 2005). Even if Bullfrogs had survived out of ponds until winter, high flows could wipe them out before the next breeding season. Although native frogs (Foothill Yellow-legged frogs and Northern Red-legged frogs) have shown behavioral adaptations to unpredictable riverine environments, Bullfrogs often do poorly in flood conditions (Doubledee et al., 2003; Kupferberg, 1996).

Two Goals for Hydro-modification: Fewer Bullfrogs and More Native Species

The primary goal of filling GP1 and GP2 was to eliminate Bullfrog populations. Assessment of success is ongoing, however, based on the (1) high percentage of radios that were detected beneath the gravel after the filling, (2) the low number of Bullfrogs (one individual) detected since the filling, and (3) lack of Bullfrog breeding observed in the area the following year, the pond filling has so far been successful at reducing Bullfrog numbers. When GP0 was filled in 2012, Bullfrogs were able to move to GP1 or GP2; by contrast, after GP1 and GP2 were filled in 2015, Bullfrogs had no nearby permanent lentic water to move to. As expected, no Bullfrog egg masses were observed in GP0 in the year after GP1 and GP2 were filled. Because the water had dried by June, the lack of breeding at GP0 made sense given that breeding the previous year occurred in mid-July at GP1 and GP2. Had successful breeding occurred in GP0 during 2016 it would have had to happen several months early, and tadpoles would have been forced to metamorphose a year early or die. Metamorphosis as first year tadpoles (YoY) is unlikely but not impossible for Bullfrogs. In Sonoma County, California, Bullfrog tadpoles were observed metamorphosing in their first year only when the egg masses were laid very early, around April. On Vancouver Island (British Columbia, Canada), a coastal area with a mild climate similar to, but slightly cooler than northwestern California, no Bullfrogs were observed metamorphosing as YoY tadpoles (Cook, 1997, Govindarajulu, 2006). Although I did not survey GP1 and GP2 for egg masses in the spring of 2015, no YoY tadpoles were observed in these ponds until August 2015, when the summer egg masses hatched, so there is no evidence from 2015 or 2016 that breeding occurs this early on the lower Mad River. Coastal northern areas, such as northwestern California, may not meet minimum temperature requirements for spring breeding or YoY metamorphosis, so the lack of permanent water in the year after pond filling was probably an important factor in the small number of Bullfrogs detected that year.

The secondary goal of filling the study ponds was to create seasonal wetland for native amphibian species. No amphibian species were found using either GP1 or GP2 in the year after filling. Observation of these wetlands over the coming years will help to determine if the secondary goal of increased habitat for native species was met. There were limited changes in GP1 and GP2 that would foster native amphibian populations in the year following hydro-modification. However, because vegetation recruitment takes time, GP0, which was filled three years prior to GP1 and GP2, may provide a glimpse into the future of these wetland sites. In the summer of 2016, there was emergent vegetation at GP0. In addition, the trees on the periphery of GP0 provided shade, and two pieces of large woody debris in the wetland created a combination of covered and open water habitat. GP0 was used for breeding by Pacific Chorus Frogs (egg masses and tadpoles observed). Only three adult Red-legged Frogs were ever observed at GP1 and GP2 prior to hydro-modification, however, this count may not be a reliable indicator of the ability of the new wetland sites (GP0, GP1, and GP2) to support Red-legged frogs. Observations of adults were from the summer (non-breeding) season, when Red-legged frogs are known to disperse from breeding sites, so summer abundance at ponds would be expected to be lower than winter abundance (Fellers & Kleeman, 2007). In the winter after the ponds were filled, I observed juveniles in GP0 from January until May. I observed recently metamorphosed Foothill Yellow-legged Frogs in GP1 and GP2 throughout the summer prior to pond filling. Though Foothill Yellow-legged Frogs are a riverine species, juveniles used GP0, GP1, and GP2 as long as there was water and vegetation in those areas.

Although GP0 is potentially a good predictor of certain aspects of the future state of GP1 and GP2, there are several key differences between all three sites. Most important is GP0's placement on the high floodplain (Figure 9). GP0 is located further back on the river bar, so is buffered from high winter flows that could wash out ponds closer to the river bar. During high flows in the winter of 2015, GP2 was completely filled with sediment and gravel from the river. Its placement on the river bar means that this could happen again in any year with high enough flows. Due to this filling by sediment, a seasonal wetland is unlikely to form there in the future. GP1 was in between GP0 and GP2 with respect to distance up the river bar, so it did not fill in with sediment as dramatically as did GP2. GP0 had a significant amount of vegetation growth over the spring and summer of 2016 that was not seen in GP1, even though water was able to collect through the winter in both sites. The increased time since hydro-modification has given plants in GP0 more time to re-colonize the area. Additionally, GP1's relative proximity to the river channel means that wetland plants may take longer to colonize the area, because seedlings are subject to winter floods and scouring more than they are in GP0. If the relative amounts of emergent vegetation in the ponds prior to filling is indicative of the amounts that could eventually persist, then the GP1 site may be able to sustain wetland vegetation better than the GP2 site would have been able to. Due to their varying positions on the river bar, GP0 is likely a good predictor for the habitat to be expected in the GP1 site, but not the GP2 site, over the next several years.

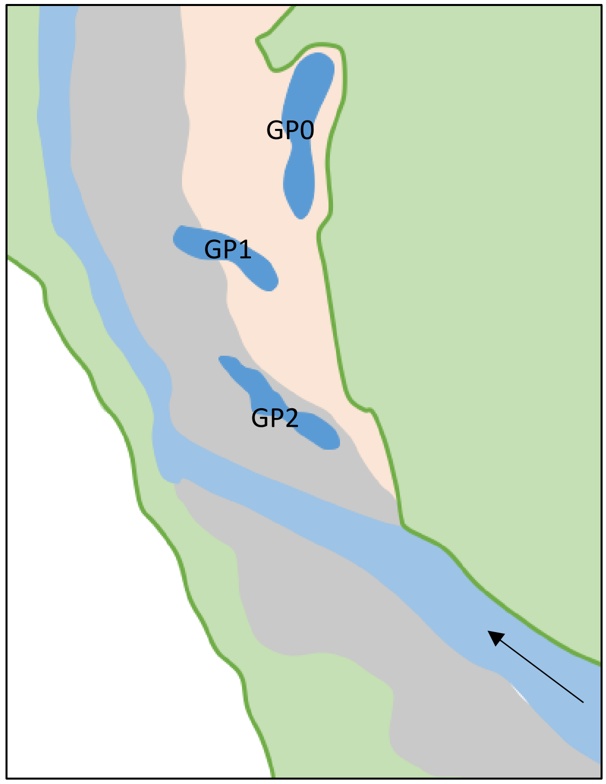

Figure 9. Pond placement in relationship to the Mad River (light blue, black arrow indicates direction of flow). GP0 is furthest from the river and is least likely to be washed out in high flows. GP2 was located fully on the gravel bar and was closest to to the river. Green = partially to mostly vegetated; beige = high floodplain, mostly bare dirt mixed with gravel; grey = gravel bar

A full evaluation of pond filling as a method of Bullfrog control will take longer than a single year, although the apparent absence of Bullfrog populations in the area during the year following filling is promising. Continued monitoring will give a better idea of how long, if ever, it will take filled ponds to become high quality seasonal wetland habitats used by native amphibians. Hydro-modification could be especially effective in circumstances similar to those in my study. It may be useful in areas where Bullfrogs are so abundant that individual removal is not feasible. Limited nearby habitat will reduce survivorship of escaped Bullfrogs. Where Bullfrogs have excluded native species, hydro-modification may be a better option than individual removal, since there will be little risk to natives. When Bullfrog-occupied ponds are also trapping native fish species there may be more motivation to fill the pond and prevent future fish trapping. If the morphology of the river suggests the pond may be filled naturally during high flows, then artificial filling may not be necessary.

My study offers a more complete picture of factors that should be considered when planning a Bullfrog eradication effort. Many eradication studies often focus solely on whether an eradication technique effectively eliminates populations. However, effectiveness could be improved by using information on phenology and movement to inform eradication timing. Especially in the case of hydro-modification – which is a punctuated, not continuous, effort – timing becomes critical. Because Bullfrog phenology varies considerably over their large range, care should be taken to consider local timing of relevant life events, including whether a dispersal is expected to occur at any time in the year.

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APPENDIX A

Appendix A. Summary of information for all radio tracked Bullfrogs. SVL = snout vent length. Sex/Stage represents life stage and sex (j = juvenile for sexually immature individuals; m = adult male; f = adult female). The 95% HR area is the size of the kernel density home range in hectares and the number of points used to determine the home range is given in the next column; for frogs with less then 30 location points no home range was estimated. Frogs that switched ponds have the original, then final pond listed in the "Pond" column. H-value = the smoothing parameter used to create the home range. Abbreviations for Frog Fates are: Buried = frog killed due to pond filling; Predated = frog killed by a predator before the end of the study; Recap = frog recaptured and radio removed in the week prior to pond filling; Remove = belt removed early due to abrasions on frog; Battery = frog's radio failed early.

Frog #	Weight (g)	SVL (mm)	Sex/ Stage	95% HR area (m^2)	# of Points	Pond	H – value	Frog Fate
011	29	65	j	1670	70	GP1	3.52	Buried
031	42	70	j	-	14	GP2	-	Predated
049	60	70	j	570	53	GP1	1.94	Recap
071	58	85	f	1450	55	GP1	3.24	Buried
091	82	88	f	3150	30	GP2	5.85	Removed
912	64	78	f	2550	30	GP1	6.79	Recap
111	37	69	j	1930	66	GP1	4.45	Buried
131	47	78	f	-	5	GP2	-	Predated
151	41	65	j	1400	49	GP2	2.74	Buried
171	36	67	j	1400	36	GP1	2.24	Predated
191	42	79	m	1590	28	GP2	4.13	Predated
208	46	73	j	690	41	GP2	1.99	Battery

Frog #	Weight (g)	SVL (mm)	Sex/ Stage	95% HR area (m^2)	# of Points	Pond	H – value	Frog Fate
231	31	65	j	990	40	GP2GP1	2.54	Battery
248	50	71	j	4710	42	GP2GP1	8.63	Battery
271	45	74	j	1880	41	GP1	4.65	Buried
291	38	96	m	1670	61	GP1	4.58	Buried
309	40	76	j	350	60	GP1	1.36	Buried
329	29	70	j	2250	62	GP1	4.64	Battery
347	88	95	m	1400	53	GP1	4.02	Battery
371	34	71	j	1550	72	GP1	3.61	Buried
389	35	62	j	1200	69	GP1	3.33	Buried
409	48	80	m	990	49	GP2GP1	2.85	Buried
431	49	83	f	620	53	GP1	2.37	Recap
449	45	88	m	1930	66	GP1	4.08	Buried
469	60	70	j	1790	63	GP1	3.58	Recap
489	29	66	j	1070	65	GP1GP2	2.85	Buried
511	72	75	j	280	67	GP1	5.68	Buried
531	79	82	f	2210	61	GP1	5.51	Buried
549	32	59	j	-	13	GP2	-	Buried
569	41	69	j	420	40	GP1	2.33	Buried

APPENDIX B

Appendix B. Summary of native and introduced species found using GP1 and GP2 throughout the tracking season. Species that were breeding in the ponds are denoted with *. Lotic species that became traped in the ponds are denoted with +.

Latin Name	**Common Name**	**Range status**
*Rana aurora**	Northern Red-legged Frog	native
Rana boylii	Foothill Yellow-legged Frog	native
*Anaxyrus boreas**	Boreal Toad	native
*Taricha granulosa**	Rough-skinned Newt	native
*Pseudacris regilla**	Pacific Chorus Frog	native
Thamnophis sp.	Gartersnake	all native
Oncorhynchus mykiss +	Steelhead (all juveniles)	native
Catostomus occidentalis +	Sacramento Sucker	native
Entosphenus sp. +	Lamprey (all ammocetes)	all native
Gasterosteus aceuleatus. +	Stickleback	all native
Gambusia affinis +	Mosquitofish	introduced
Pacifastacus leniusculus	Signal Crayfish	introduced
Multiple genera possible	Freshwater Mussel	unknown

APPENDIX C

Appendix C. Summary of native and introduced plant species identified in the GP0 pond site.

Latin Name	Common Name	Range status
Alisma triviale	Northern Water Plantain	native
Alnus spp.	Alder	all native
Centarium tenuiflorum	Slender Centuary	introduced
Equisetum palustre	Marsh Horsetail	native
Hordeum depressum	Dwarf Barley	native
Mentha pulegium	Pennyroyal	introduced
Ranunculus repens	Creeping Buttercup	introduced
Rubus armeniacus	Himalayan Blackberry	introduced
Rumex crispus	Curly Dock	introduced
Rumex spp.	Dock	unknown
Salix melanopis	Dusky Willow	native
Typha spp.	Cattail	unknown

APPENDIX D

Appendix D. Summary of previous Bullfrog movement studies. Method refers to how Bullfrogs were tracked. Sex/stage lists numbers of individuals and their sex and life stage (if reported by the authors): M = male, F = female, J = juveniles. Season and climate reports when tracking occurred and gives a general description of temperature and precipitation for that region. Movement findings summarizes the movement data from each study; not all studies used the same metrics to describe movement patterns. Results given in feet or miles have been converted to meters for ease of comparison.

Authors	**Method**	**Sex/ Stage**	**Region**	**Season and climate**	**Movement findings**
Berroneau et al., 2007	Telemetry	M = 18 F = 7	southwest France	September – June, Cool/rainy winter, warm/dry summer	Home range: fall = 1,447 m^2, winter = 0.03 m^2, spring = 15,668 m^2. Bullfrogs dispersed from ponds after hibernation but returned a month later.
Currie & Bellis, 1969	Mark-recapture	M = 65 F = 66	Ontario, Canada	August, warm/rain	Estimated a mean 2.6 m activity radius. When populations were dense, activity radii were smaller.
Raney, 1940	Mark-recapture	M = 106 F = 48 J = 83	New York State	Summer, warm/rain	Most movements (within ponds) $\leq$ 50 m. Max distances from ponds: M = 106 m, F = 88 m, J = 18 m.
Roninger, 2008	Telemetry	F = 5 J = 14	Wood River, OR	September – November, cool/rain	Tracked frogs to their overwintering locations. Distance from capture to last location ranged from 50 to 1,200 m.

Authors	Method	Sex/ Stage	Region	Season and climate	Movement findings
Stinner et al., 1994	Telemetry	6, sex/ stage not reported.	Summit Co., Ohio	October – May, -8 to 20° C, dry	Movements ranged from 0 to 100 m. Highest activity in October and April.
Willis et al., 1956	Mark-recapture	263, sex/ stage not reported.	Missouri	June – July, warm/rain	8% of tagged frogs moved between ponds. Ponds were 160 to 1,600 m apart. Observed very small juveniles away from ponds.