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An effective method for long-term control of American bullfrogs syntopic with special-status native amphibians in California, USA

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Abstract: American bullfrogs (*Lithobates catesbeianus*) are invasive in western North America and are well established in California, USA, where they are widespread. This invasive species has been implicated in the decrease of native amphibian populations and is believed to have contributed to the decline of threatened and endangered amphibians regionally. We utilized air rifles, tin alloy pellets, and 2 shooters to systematically control *L. catesbeianus* in both lentic and lotic habitat types within 2 counties in California. We visited sites monthly (April through November) for approximately 8 and 14 years to lethally target and remove *L. catesbeianus* from aquatic habitat. The use of air rifles facilitated selective targeting; adult *L. catesbeianus* were initially targeted to break the reproductive cycle, with subadult *L. catesbeianus* secondarily targeted and removed when possible. Egg masses, when encountered, were also removed. Habitat type (lentic vs. lotic) did not appear to affect the results of the technique used. We considered *L. catesbeianus* under control when observed breeding adults were reduced by approximately 95% from original estimates, which occurred within 36 months for both sites. California red-legged frogs (*Rana draytonii*) were observed recolonizing the lotic site 12 months before *L. catesbeianus* numbers reached control levels. At the lentic site, foothill yellow-legged frogs (*R. boylii*) colonized and reproduced in a pond 31 months following the onset of *L. catesbeianus* control. This technique appears to be highly efficient for *L. catesbeianus* control, which, if conducted effectively, may support colonization or recolonization of habitat by native anurans.

Key words: air rifle, behavior, bullfrog, control, *Lithobates catesbeianus*, invasion, native, tin alloy pellets

The American bullfrog (*Lithobates catesbeianus*) is native to the eastern United States but has been introduced widely throughout the world, in part due to its value as a food source (Adams and Pearl 2007). This species is adapted to a wide range of climatic conditions and is now well-established in parts of Europe (Lanza 1962, Banks et al. 2000), Asia (Kim and Ko 1998, Wu et al. 2004), South America (Borges-Martins et al. 2002, Hanselmann et al. 2004), North America—outside of the United States (Mahon and Aiken 1977, Green and Campbell 1984, Ortíz-Serrato et al. 2014), and in western North America (Bury and Whelan 1984), including Hawaiʻi, USA (Viernes 1995). Where *L. catesbeianus* has been introduced, it has typically become highly invasive, and the presence of *L. catesbeianus* is often associated with a decline of native amphibians (Moyle 1973, Kiesecker and Blaustein 1997, Kupferberg 1997, Kiesecker and Blaustein 1998, U.S. Fish and Wildlife Service 2002). In western North America, the displacement of native frogs by introduced *L. catesbeianus* is pervasive, and several mechanisms may contribute to the success of *L. catesbeianus* (Adams 1999, Adams and Pearl 2007, Witmer et al. 2015). Historically, ponded water was an uncommon natural feature in much of the American West, but the creation of stock ponds, reservoirs, and detention ponds has altered the landscape in such a way as to facilitate the spread of many amphibians, including *L. catesbeianus*, into previously unoccupied areas (sensu Wilcox et al. 2015). In their comprehensive review, Adams and Pearl (2007) suggested that invasive *L. catesbeianus* were a conservation concern for many reasons, including their roles as: (1) disease vectors, (2) voracious predators of other wildlife species, and (3) direct and indirect competitors with native anurans. All of these concerns may be compounded by the putative difficulty of controlling *L. catesbeianus* populations (Adams and Pearl 2007, Witmer et al. 2015).

The biphasic life history (Wilbur 1980) of *L. catesbeianus* presents challenges to their control, as well as potential opportunities (Govindarajulu et al. 2005). Control of each life history stage requires different techniques and strategies, and variability in habitat may add complexity to any control effort, particularly when native amphibians are present. Control efforts directed at *L. catesbeianus* have included indirect removal through habitat manipulation, direct removal, or a combination of both (Adams and Pearl 2007). Indirect removal typically targets the larval stage of *L. catesbeianus* by draining breeding ponds (Adams and Pearl 2007). Timing of pond draining is critical because sympatric native amphibians may be negatively affected by the draining process (Alvarez et al. 2013). In California, USA, pond-draining efforts to control *L. catesbeianus* are often timed for late fall after native amphibians have undergone metamorphosis and dispersed from the pond before the onset of rainwater or ground water recharge. However, recent observations suggest that at least 2 special-status amphibian species in California may overwinter as larvae, causing regulatory agencies to reconsider permitting pond draining where special-status amphibians are potentially sympatric with *L. catesbeianus* (Fellers et al. 2001, Alvarez 2004, Alvarez et al. 2013, Wilcox et al. 2015). Further, *L. catesbeianus* are semi-aquatic (Lemenager et al. 2021) and may leave water bodies to aestivate when ponds are drained, only to return and reproduce when winter rains refill pond basins.

Direct removal of *L. catesbeianus* implies elimination or direct mortality of individual frogs from wild populations, including larvae and, when possible, complete egg masses. Egg masses may be directly removed once they are deposited, but *L. catesbeianus* breed over a very long period of time, and sustained vigilance may be difficult to maintain (Willis et al. 1956). Individual larvae can be removed, or numbers may be reduced by seining, hand netting, and trapping. Post-metamorphic frogs (metamorphs) may be hand-captured (Govindarajulu 2004), trapped (Snow and Witmer 2011), subjected to chemical control (Witmer et al. 2015), gigged, electro-shocked (Orchard 2011), or shot with an appropriate projectile (Rosen and Schwalbe 1995). Each of these methods involves a considerable commitment in labor to achieve control, with costs dependent upon technique employed, site accessibility, and labor efficiency (Orchard 2011), as well as habitat complexity (J. Alvarez, personal observation).

For invasive species control to become widespread as a method to restore native amphibian populations, control efforts must be simple, unencumbered by specialized equipment, repeatable over many scenarios, and cost-effective (Donlan et al. 2003). Through the expediency necessitated by contract agreements, we developed a simple, efficient method of direct removal of adult *L. catesbeianus* that has produced long-term control in 2 commonly invaded habitats, at multiple sites over >20 years, in northern California. Here we describe the events of 2 more-typical efforts that involved control of *L. catesbeianus* where they were syntopic with special-status amphibians, in situations likely to be encountered by most eradication efforts: a perennial stream, and a small agricultural reservoir. We based our strategy on exploiting certain natural history traits of *L. catesbaeianus* behavior that leave them vulnerable to intensive hunting pressure. Our control program is based on the premise that *L. catesbeianus* life history is strongly r-selected (MacArthur and Wilson 1967, Pianka 1970), in which high numbers of offspring are produced but few survive to adulthood (Wilbur and Collins 1973, Wilbur 1980). Therefore, we focused control efforts on adult frogs—those with a snout-to-urostyle length of 70 mm or greater (Urbina et al. 2020)—because they represent the breeding potential of the invasive population, the source of propagule pressure (Simberloff 2009) of invading *L. catesbeianus*. Breeding adult *L. catesbeainus* are conspicuous due to their large size, the audible lowing of calling males, and aggressive defense of breeding territories simplifies their detection (Wells 1977).

We hypothesized that (1) targeting the sexually mature adults would be most efficient because they are least numerous and most conspicuous; (2) *L. catesbeianus* are promiscuous lek breeders (Wells 1977), and thus the removal of dominant males passively removes gravid females from the pool of breeders as male numbers are reduced; and (3) by repeatedly visiting sites over the entire breeding season, we simulated an apex predator keying on the breeding adult *L. catesbieanus*, effectively stifling propagule pressure (Simberloff 2009), essentially engaging in the purposeful overhunting by humans that has facilitated many extinctions.

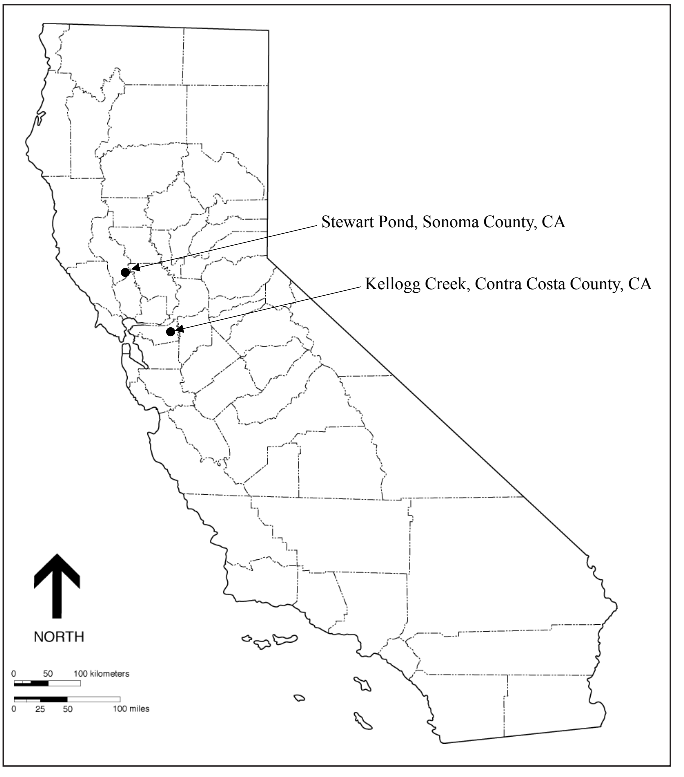

Figure 1. General locations of the Kellogg Creek and the Stewart Pond bullfrog (Ranidae) control sites.

Methods

A 2-person team visited each site once per month from April through November, a time in California that marks warm temperatures and the cessation of heavy rains (Schoenherr 1992). This level of effort was dictated by the constraints of the project before our arrival. Control efforts began with a visual assessment of the site conditions (i.e., vegetation type; habitat complexity; *L. catesbeianus* numbers and age/size classes; and presence of other anurans). During each site visit, a shoreline transect was walked by the team to count *L. catesbeianus*; relative abundance of sympatric herpetofauna were also recorded when encountered. Due to our limited mandate to control only *L. catesbeianus*, a clear development and assessment of the baseline population of any non-target species was not performed.

Each team member was armed with an air rifle and binoculars. We used 0.177-caliber break-barrel air rifles capable of firing a pellet at a minimum of 365 m per second (1,200 feet per second). Break-barrel air rifles afford a consistent velocity that might be difficult to achieve with pump-action and CO_2 canister-style air rifles. Consequently, they are the only style of air rifle authorized by the California Department of Fish and Wildlife (CDFW), in conjunction with a Scientific Collecting Permit and Memorandum of Understanding to collect *L. catesbeianus*. All air rifles were equipped with 3x9 variable scopes capable of focusing on a target at a minimum distance of approximately 2.5 m. We sighted-in the scoped rifles before each visit. We used tin alloy pellets (RWS HyperMax, RUAG Ammotec, Sulzbach-Rosenberg, Germany; or H&M domed lead-free, Hatsan, USA, Inc., Rogers, Arkansas, USA) to avoid lead or copper contamination of waterways, and to avoid lead ingestion by scavengers or predators that might encounter a dead or wounded *L. catesbeianus* (sensu Pauli and Buskirk 2007).

Study area

Our lotic site was Kellogg Creek, a perennial stream (37°52′15″N, 121°42′00″W) in eastern Contra Costa County, California (Figure 1). In the 0.5-km reach where we conducted control efforts, stream flows were regulated by upstream releases from the Los Vaqueros Reservoir (0–5 cubic feet per second [cfs]; typically, 1–2 cfs), with flows being relatively constant, even outside of the rainy season. The stream channel ranged from 2–7 m wide and was populated with emergent and submergent vegetation such as cattail (*Typha* sp.), California bulrush (*Scheonoplectus californicus*), perennial pepperweed (*Lepidium latifolium*), mannagrass (*Glyceria* spp.), and spikerush (*Eleochorus* sp.). In some portions of the stream, the immediate upland areas were comprised of tall banks that rose to 6 m above the stream surface, but in much of the reach we were able to walk to the stream edge. Water depth ranged from 0.5–2.5 m but was highly variable due to numerous American beaver (*Castor canadensis*) dams. Sympatric herpetofaunal species that occurred in the portions of Kellogg Creek unoccupied by *L. catesbeianus* included *R. draytonii*, Pacific treefrog (*Pseudacris regilla*), western toad (*Anaxyrus boreas*), the federally and state threatened California tiger salamander (*Ambystoma californiense*), and a declining turtle species, the southwestern pond turtle (*Actinemys pallida*).

Our lentic site, Stewart Pond, was a perennial reservoir (38°38′47″N, 122°39′38″W) in eastern Sonoma County, California (Figure 1). The pond basin was fed by 3 intermittent streams and attained a depth of approximately 8 m before it could spill over. At full capacity, it had a surface area of approximately 0.8 ha and was primarily used for recreation and irrigating vineyards. Emergent aquatic vegetation was comprised of a few discreet patches of narrowleaf cattail (*T. angustifolia*), dallis grass (*Paspalis dilitatum*, *Glyceria* spp.), and *Eleochorus* sp., which lined much of the shallow perimeter. At the initiation of the control efforts, the site was occupied by *L. catesbeianus* and what appeared to be a large number (ca. ≥50 individuals) of northwestern pond turtles (*Ac. marmorata*). Adjacent habitats supported *P. regilla*, *An. boreas*, *Ac. marmorata*, and a declining frog species, the foothill yellow-legged frog (*Rana boylii*).

Site visits commenced in the late afternoon with each of the 2-member team carrying an air rifle and walking side-by-side around or along the project shoreline. Starting in daylight allowed re-acquaintance with the site, including recognition of possible fluctuations in water level, obstructions to navigate (i.e., fallen debris, cattle [*Bos taurus*] presence, exposed holes, etc.), and an assessment of changes in frog locations, numbers, and size classes (Fellers and Kleeman 2006). We visually searched with 8x42 binoculars and simultaneously listened for frog vocalizations. When a frog was visually encountered, each team member was required to independently confirm the target as *L. catesbeianus*. If both members did not confirm, the target was bypassed. We passed over unidentifiable targets knowing we would likely encounter them later in the survey, or on a subsequent visit. A shot was taken only when both team members confirmed the target as *L. catesbeianus*. The non-shooting member used binoculars to observe the targeted *L. catesbeianus* before, during, and immediately following the shot. In this way, the observing member could either confirm a kill or inform the shooting team member where the shot landed and how to correct the next shot, if presented. Most shots were taken within 10 m from shore, allowing accurate placement of lethal shots. When the positioning of *L. catesbeianus* offered a poor, potentially sublethal shot, the opportunity was bypassed in anticipation of being presented with a better one on a subsequent encounter.

After nightfall, when frog detection is at its highest, we repeated the shoreline transect 2 times. We used headlamps/flashlights to locate frogs, primarily from light reflected off the frog's tapetum lucidum (Corben and Fellers 2001). We used a flashlight, held along the bottom of the fore stock of the air rifle, to locate the target in the scope and shoot accurately. Headlamps obscure the objective lenses of scoped rifles, so the team member shooting switched off the headlamp to shoot, and the observing member watched the target through binoculars, as in day shooting.

On each visit, to control the possible transmission of infectious diseases, *L. catesbeianus* carcasses that could be retrieved were collected. When possible, *L. catesbeianus* carcasses were collected using a hand-held net and buried following CDFW regulations (M. Grefsrud, CDFW, personal communication). We defined control as: (1) no detected egg masses, (2) no detected larvae, (3) no sign of metamorphosis in the summer/fall of the year, and 4) no adults detected during 2 consecutive visits, along with the previous 3 conditions.

Results

Post-event monitoring results (7 years at the lentic site; 14 years at the lotic site) indicate no *L. catesbeianus* populations have re-established after initiation of our control protocol. At Kellogg Creek, we estimated the initial *L. catesbeianus* occupation within a range of 200–300 adult and juvenile *L. catesbeianus*, as well as hundreds of larvae. No native anurans were initially detected, but <5 individual *Ac. pallida* were ob-

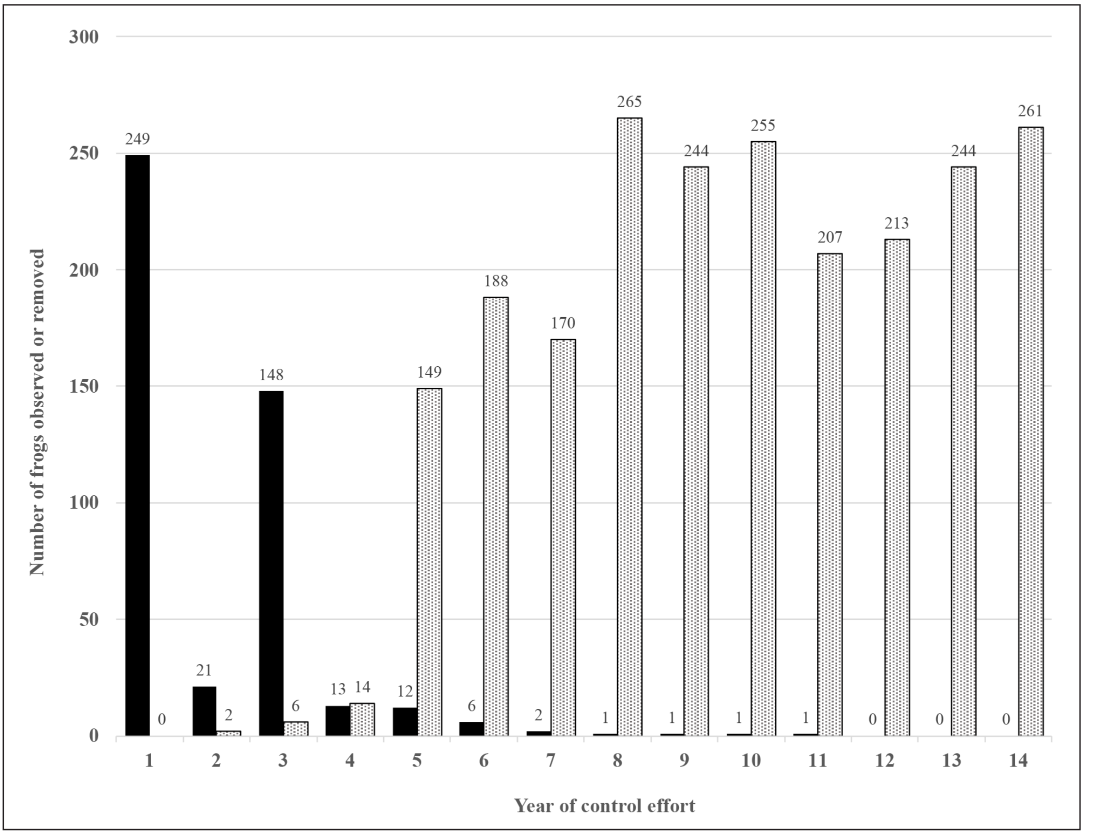

Figure 2. Trends in American bullfrogs (*Lithobates catesbeianus*) removed (black) versus California red-legged frogs (*Rana draytonii*) observed (gray) in Kellogg Creek, over a 14-year period of control efforts in Contra Costa County, California, USA.

served. Control efforts brought a precipitous decline in *L. catesbeianus* adults between years 1–2 and 2–3 (Figure 2); the number of observed *L. catesbeianus* was reduced by 85–95% in the first year. Detections of all age/size classes of *L. catesbeianus* declined to <5 per visit after 24 months. A total of 3 *L. catesbeianus* egg masses were found in the first 3 years of control, but no egg masses were detected thereafter. During the second year of control efforts, a reproductive effort may have gone undetected, resulting in a population spike of 142 post-metamorphic *L. catesbeianus*, with a subsequent decline during continued control efforts. In the ensuing 10-year period, we observed no juvenile *L. catesbeianus*. During control years 7–11, we observed and removed an average of 0.75 *L. catesbeianus* per year, with zero detected in years 12–14.

We observed an ecological release (Paine 1966) in native species as *L. catesbeianus* numbers declined. Adult *R. draytonii* recolonized the Kellogg Creek site the first year of control efforts, and reproduction was evident by the second year when their larvae became visible (Figure 2). Through consistent reproductive efforts, *R. draytonii* established a stable population by year 5 of *L. catesbeianus* control efforts. Observations of *Ac. pallida* also increased in Kellogg Creek during our control efforts, with a notable increase in observations of neonates from zero to >1 year.

At Stewart Pond, we initially estimated the population of *L. catesbeianus* to be approximately 2,500–3,000 adult and post-metamorphic frogs, but no larvae were detected. No native anurans were detected, but adult *Ac. marmorata* were abundant (≥50 individuals). By the end of the second year of control efforts, *L. catesbeianus* were in a steep decline (Figure 3). Cumulative observations during the third year of control included only 11 adults (all were removed), and no obser-

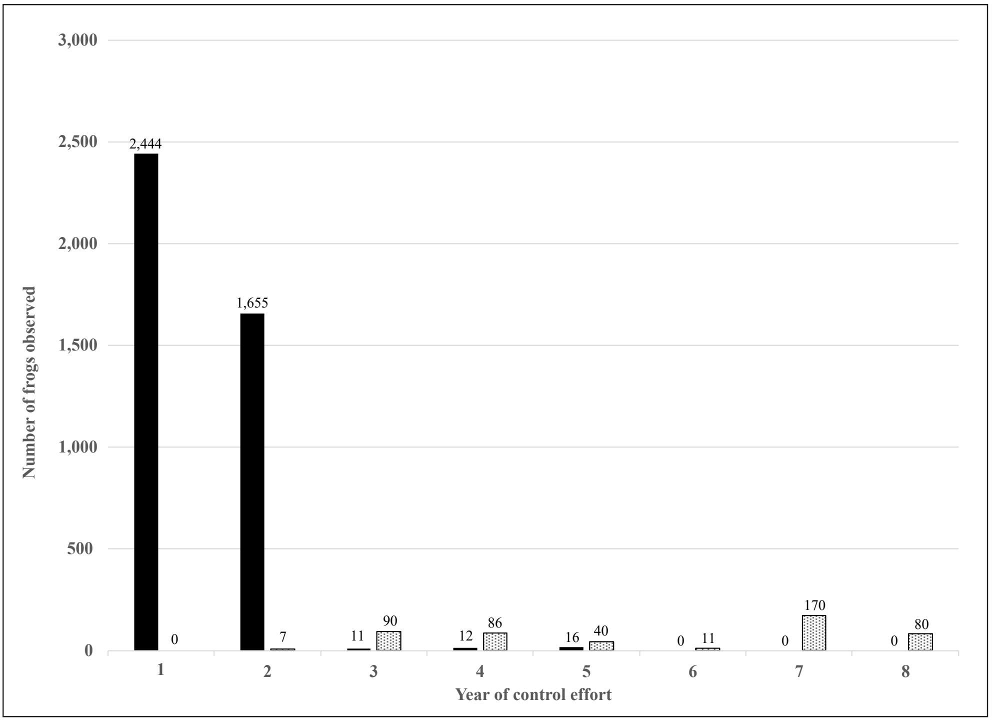

Figure 3. Trends in American bullfrogs (*Lithobates catesbeianus*) observed (black) versus foothill yellow-legged frogs (*Rana boylii*) observed (gray), over an 8-year period of control efforts in the Stewart Pond, Sonoma County, California, USA.

vations were made of post-metamorphic frogs, larvae, or egg masses. In years 4–8 (26 subsequent site visits), we did not detect adult *L. catesbeianus* visually or aurally at the Stewart Pond site.

Again, we observed an ecological release (Paine 1966) during control of *L. catesbeianus* at Stewart Pond when we observed a recolonization by the native anurans *R. boylii*, *P. regilla*, and *An. boreas*, including breeding of these species, which was not observed before control efforts commenced. The appearance of *R. boylii,* a California Species of Concern (Jennings and Hayes 1994, Thomson et al. 2016) and a putative stream obligate, was a surprise because the mandate for the Stewart Project focused on the restoration for *R. draytonii* (Wilcox and Alvarez 2019). We also noted a distinct increase in post-emergent neonate *Ac. marmorata*, which increased from zero at the onset of the control efforts to 3–8 per visit 2 years after *L. catesbeianus* were at undetectable levels.

Discussion

By employing precision equipment and well-trained, 2-person teams to control *L. catesbeianus*, we were able to develop an effective technique that minimizes time and effort compared to most others. Although each site described here was geographically and hydrologically disparate, we achieved control (approximately a 99% decrease) of adult *L. catesbeianus* after 3 years at each site (Figures 2 and 3). Our data suggest that *L. catesbeianus* can be reduced to levels that are undetectable in a short period, and our observations suggest that *L. catesbeianus* were not able to effectively recolonize, for reasons that were not determined, despite bullfrogs being present locally and regionally. We acknowledge that we did not test hypotheses, nor did we test rigorous statistical models, so our data are anecdotal observations, and all analyses were *a posteriori*. However, we made a concerted effort to accurately estimate numbers, and we sustained our control efforts over an unusually long period of years considering the length of most efforts. We further acknowledge that visiting a site once per month allows time for breeding adults to oviposit in the intervening time period between site visits. Our targeting of *L. catesbeianus* >70 mm is directed at breaking the reproductive cycle by removing reproductive adults (Urbina et al. 2020), but some breeding can still occur on some sites. Our experience suggests intense pressure (removal of 100 frogs in a single visit) may negatively affect breeding behavior at some sites—reduce successful breeding, as determined by a reduced or complete absence of post-metamorphic individuals in the second and third years of control (J. Alvarez, unpublished data).

We used a method of control that exploits the *L. catesbeianus* r-selected life history (MacArthur and Wilson 1967), and we exploited the conspicuous physical and behavioral traits that make *L. catesbeianus* most vulnerable to detection and removal. Models tested by Govindarajulu et al. (2005) on Vancouver Island, British Columbia, Canada, indicated that targeting the juvenile stage was most efficient for controlling *L. catesbeianus*. We contend that targeting the sexually mature adults is most efficient because they are the only stage capable of reproduction; they are behaviorally conspicuous; and *L. catesbeianus* are promiscuous lek breeders, and thus the removal of dominant males passively removes gravid females from the pool of breeders as male numbers are reduced. By repeatedly visiting sites, we simulated an apex predator keying on the life history stage that had the greatest potential for rapidly increasing its population (Wells 1977).

By targeting breeding *L. catesbeianus*, team-shooting is a form of direct removal that involves less cost, planning, and risk of failure than indirect control methods such as pond draining. Pond draining can be labor-intensive (cost-prohibitive) due to the wide variation in size, basin shape and volume, vegetation, and accessibility of water bodies, and a positive outcome is not guaranteed because larvae can survive long periods in unseen pockets of water while the pond basin refills from seeps or precipitation (J. Alvarez, personal observation). Further, the semi-terrestrial adult *L. catesbeianus* (Lemenager et al. 2021) often leave the pond during the draining period, simply to return to reproduce when ponds refill. Chemical control could be more efficient and less expensive, but this method has not been extensively field-tested (Snow and Witmer 2011, Witmer et al. 2015).

We believe team shooting is more efficient than hand capture (Govindarajulu et al. 2005) and gigging because it does not involve wading, which often disturbs adjacent individuals, and no euthanasia is necessary since frogs are normally dead before handling. Other methods, like trapping and electro-shocking, may be a relatively comparable method in terms of efficiency, but the technology is specialized and expensive; they may be most efficient when deployed from a boat, limiting its application to simplified pond habitats and appropriate streams, or larger aquatic systems (Orchard 2011). Chemical control, draining, and electroshocking may also have profound and long-lasting impacts on declining species, which is in opposition to the purpose of *L. catesbeianus* control efforts (Adams and Pearl 2007, Orchard 2011, Alvarez et al. 2017).

Team-shooting employs relatively inexpensive air rifles that are widely available and is a skill for which most people can quickly achieve a level of proficiency necessary for this work. Shooting also provides an inherent stealth advantage in that targeted frogs can be killed without disrupting other *L. catesbeianus* that may be sitting nearby. Combining a daytime hunt with a night-time hunt allows team participants the added safety of observing any changes that may have occurred in the landscape between visits (water level changes, exposed hazards), and to assess where frog activity (i.e., calling males) is focused (Fellers and Kleeman 2006). Night shooting exploits the advantage of using lights to illuminate the targets and allows the team members to approach targets more closely as they are concealed behind the beam of light (Hailman and Jaeger 1978, Buchanan 1993), thus reducing the flight distance of the frogs (Blumstein et al. 2003) and facilitating better shots. Finally, and critically, with a trained shooting team, this method can be used in the presence of native or special-status species without harming non-targets.

Management implications

Shooting alone is not likely to account for the exponential decline in *L. catesbeianus* numbers we observed, but we are at a loss to explain why this has been the case in all of our control efforts. Although we acknowledge that observational data here do not conclusively test our specific methods, we can decisively say that the method reported herein is effective at reducing *L. catesbeianus* numbers quickly and for long periods of time. Future testing of this method should be hypothesis-based to determine its efficacy and to elucidate the underlying drivers of observed results.

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