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Effects of invasive American bullfrogs and their removal on Northwestern pond turtles

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ABSTRACT

The American bullfrog (*Rana catesbeiana*) is an invasive species globally significant for its role as a generalist predator in freshwater systems. Native turtles are among the species eaten by bullfrogs, and turtle populations are slow to recover from this impact. We examined the effects of bullfrogs and their removal on Northwestern pond turtles (*Actinemys marmorata*) at four sites in Yosemite National Park. From 2016 to 2022, we monitored turtle populations in two sites where bullfrogs were present and two where they have been absent. We removed 12,317 bullfrogs, larvae, and whole egg masses from one site and 4067 from the other, reaching near complete eradication by 2019. We captured just large adult turtles where bullfrogs were present compared with all sizes where bullfrogs were absent. Prior to near complete eradication, juvenile turtles were only found with bullfrogs when they were recovered from bullfrog stomachs. Turtles at bullfrog present sites were 26–36 % larger and 76–97 % heavier than turtles from bullfrog absent sites. Turtle abundance and densities were also 2–100 times higher at bullfrog absent sites. We captured the first juvenile turtles at bullfrog present sites only after reaching near complete bullfrog eradication in 2019. Altogether, our study shows a prolonged lack of juvenile turtle recruitment where bullfrogs were present but offers hope that bullfrog control may succeed in recovering turtle populations by easing predation pressure on hatchlings and juveniles. Our results indicate that bullfrog eradication efforts may be necessary to ensure persistence of at-risk species like native turtles.

1. Introduction

Invasive species are one of the leading drivers of global species decline (Wilcove et al., 1998; Butchart et al., 2010), and managers are increasingly faced with the daunting task of mitigating effects of invasive species on native ecosystems. Left unmitigated, invasive species can alter species assemblages and interactions in ecosystems, in many cases threatening native species with extinction (Bellard et al., 2016; Blackburn et al., 2019). Among the most threatened ecosystems are freshwater systems, which support >100,000 animal species on <1 % of Earth's total surface (Ricciardi and Rasmussen, 1999; Dudgeon et al., 2006; Balian et al., 2008). Given declines in freshwater biodiversity, the rise in non-native species introductions has great implications for native species persistence (Mooney and Cleland, 2001; Dudgeon et al., 2006).

One invasive species distributed widely outside its native range with significant ecological impacts is the American bullfrog (*Rana* [*Lithobates*] *catesbeiana*, hereafter 'bullfrog'). Bullfrogs can quickly establish in new areas, with their populations reaching tens of thousands of individuals (Bury and Whelan, 1984; Louette et al., 2012). They are also opportunistic predators, known to consume diverse taxa, including insects, crustaceans, amphibians, reptiles, fish, small birds, and mammals (Korschgen and Baskett, 1963; Bury and Whelan, 1984; Hothem et al., 2009; Jancowski and Orchard, 2013). Their indiscriminate diet has led bullfrogs to be implicated in the disappearance or imperilment of many native species (Moyle, 1973; Bury and Whelan, 1984; Lawler et al., 1999; Adams and Pearl, 2007).

Yosemite National Park in the western United States, renowned for its protected wilderness, is not immune to the risks posed by invasive species. Among the park's native fauna, the Northwestern pond turtle (*Actinemys marmorata*; hereafter 'pond turtle') has seemingly disappeared from Yosemite Valley—especially in areas where bullfrogs dominated for over half a century (Kamoroff et al., 2020). In Yosemite,

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some remaining pond turtle populations co-occur with bullfrogs. Reported instances of small pond turtles in bullfrog stomachs have led some to attribute pond turtle declines at least in part to the introduction of bullfrogs (Holland, 1994; Sloan, 2012; Hallock et al., 2017; Nicholson et al., 2020; Manzo et al., 2021). Pond turtles have naturally low recruitment and high hatchling mortality, characteristics shared by many turtles globally that place them at particular conservation risk and make them among the world's most imperiled vertebrate fauna (Bury et al., 2012; Rhodin et al., 2018; Stanford et al., 2020). The addition of yet more mortality from introduced bullfrogs likely further limits pond turtle recruitment. As such, pond turtle populations that co-occur with invasive bullfrogs have been found to lack juveniles and be dominated by larger—and presumably older (sensu Sloan, 2012)—pond turtles (Nicholson et al., 2020). Effective bullfrog management may thus be an option to mitigate the impacts of bullfrogs.

Eradication is one of several strategies for managing invasive species, which can also include habitat modification, biological controls, or other strategies (Simberloff, 2002; Adams and Pearl, 2007). Eradication and control programs are often expensive, labor-intensive, require sustained efforts over long periods, and garner mixed public opinions (Genovesi, 2005; Adams and Pearl, 2007; Simberloff et al., 2013). Control can also have the unintended effect of increasing survival for remaining individuals—particularly in juveniles—causing populations to rebound and exceed pre-removal abundances (Govindarajulu et al., 2005; Zipkin et al., 2009). However, when feasible, targeted removal of invasive species can promote the return or restoration of native species (Vredenburg, 2004; Genovesi, 2005; Knapp et al., 2007; Kamoroff et al., 2020; Adams et al., 2023b), and such a strategy may be needed to recover pond turtle populations over the long-term.

The purpose of our study was to compare body size (length), condition (mass relative to length), and population structure (using size distributions) in pond turtle populations from sites with and without bullfrogs as well as to examine the response in pond turtle recruitment following active bullfrog eradication. By examining four study sites in protected Yosemite National Park, we were able to isolate the impact of bullfrogs from other conservation challenges like road mortality, poaching, agriculture, pollution, and habitat alteration. We expected pond turtle populations with decades of co-occurrence with bullfrogs would have on average, larger turtles (Sloan, 2012; Nicholson et al., 2020) and smaller population sizes than those without bullfrogs as a result of a prolonged lack of recruitment from increased predation on juvenile turtles. We also expected that reducing bullfrog numbers with eradication effort would facilitate new juvenile turtle recruitment. The results of our study should shed light on the role of invasive bullfrogs on pond turtle populations and the value of invasive species control for recovering declining native freshwater turtles.

2. Methods

2.1. Study sites

We conducted this study in Yosemite National Park, Tuolumne County, California, USA. We identified two waterbodies with co-occurring bullfrog and pond turtle populations and two waterbodies with pond turtle present only populations. We mask place names with generic location names owing to the sensitive status of the Northwestern pond turtle and to distinguish between bullfrog present or absent. The two sites with established bullfrog populations—Bullfrog Present 1 and Bullfrog Present 2—lie in the northwestern region of the park, east of Lake Eleanor and west of Hetch Hetchy Reservoir. American bullfrogs were deliberately introduced to Bullfrog Present 1 sometime in the mid-1970s and were well-established by 1990 (Dave Graber, pers. comm.). The exact reason for introducing bullfrogs is unknown, but for context, bullfrogs were widely introduced to the Western US—primarily as a food source for humans—beginning in the late 1800s (Snow and Witmer, 2010). Just south of these bullfrog present sites, Yosemite Valley was also the recipient of intentional bullfrog introductions in the 1950s (Cunningham, 1960; Kamoroff et al., 2020). Bullfrog Present 1 is a 2.5 ha small pond at 1530 m elevation that was originally a spring and formed when water filled the area after it was excavated and used as a borrow area in the 1930s. Bullfrog Present 1 was stocked with non-native Rainbow trout (*Oncorhynchus mykiss*) and Brook trout (*Salvelinus fontinalis*) from 1939 to 1987 with over 55,000 trout. Today, stocking no longer occurs and Brook trout have not been observed, but Rainbow trout are still known to occur at Bullfrog Present 1 in small numbers. Bullfrog Present 2 is a glacially formed 7.8 ha lake at 1557 m elevation that lies 1.45 km south of Bullfrog Present 1 and is accessible only by off-trail hiking. It is unknown whether bullfrogs were similarly deliberately introduced to Bullfrog Present 2 or whether individuals immigrated from Bullfrog Present 1. Bullfrog Absent 1 is a 5.78 ha shallow lake at 1596 m elevation that dries partially in late Fall. Bullfrog Absent 2 is a smaller 0.5 ha shallow pond at 1430 m elevation that likewise dries partially in early Fall. Bullfrog Absent 1 and 2 sites lie 4.73 km south of the two bullfrog present sites. There is no evidence to suggest that bullfrogs were ever present at Bullfrog Absent 1 or 2.

The four study sites are in predominantly coniferous forests with herbaceous vegetation typical of the lower montane forests on the western slopes of the Sierra Nevada Mountains (North et al., 2016). Hot, dry summers and cool, wet winters characterize the region's climate. Dominant emergent vegetation at the four waterbodies consisted of alder (*Alnus* sp.), willow (*Salix* sp.), western azalea (*Rhododendron occidentale*), dogwood (*Cornus* sp.), watershield (*Brasenia schreberi*), yellow pond lily (*Nuphar lutea*), and sedge (*Carex* sp.). Thus, in sum, the four study sites all occurred at similar elevations, in similar habitat, with similar climate, within 5 km of each other, and in a national park buffered from many contemporary conservation challenges that afflict landscapes outside park boundaries.

2.2. American bullfrog eradication effort

We removed American bullfrogs from the two Bullfrog Present sites during spring and summer months (typically May–October), 2015–2022. Due to the location of the sites, our efforts required extended backcountry camping to make the work feasible. Owing to mutable park budgets and related hiring and training constraints, the vicissitudes of weather, and the COVID-19 pandemic, our effort at the two sites varied annually and resulted in limited effort in some years. In general, we conducted visual surveys during the day to locate and scoop bullfrog egg masses using paint strainers and/or fine-mesh zoo-plankton sampling dipnets. At night, we located post-metamorphic bullfrogs (adult and juvenile) to remove using high-powered (>500 lm) flashlights and headlamps. We captured bullfrogs by use of hand captures, pole spears, dip nets, pellet air rifles, or via electro-shocking. However, the last two methods were limitedly used, and electro-shocking was abandoned after year one. Although we did not target tadpoles for removal, occasional tadpoles were removed via dip nets and turtle traps from incidental captures. Egg masses removed were placed on the bank to desiccate while adult and juvenile bullfrogs were euthanized by topical application of benzocaine (20 %) to the ventral abdomen followed by pithing as a secondary measure per 2013 AVMA guidelines (American Veterinary Medical Association [AVMA], 2013). We employed these methods while walking the perimeter of the waterbody or from inflatable boats to maneuver the inside perimeter of the waterbody and access floating islands and vegetation that harbored bullfrogs and egg masses.

We recorded the life stage and the snout-to-vent length (SVL) of all bullfrogs >100 mm SVL. We dissected bullfrogs >100 mm SVL and recorded their sex, stomach contents, and whether females were gravid or spent. Stomach contents were identified in the field to the finest taxonomic scale possible (e.g., order, family, genus, species) depending on the condition of the remains.

In addition to nighttime removal efforts, we conducted visual encounter surveys during the day to remove egg masses with dip nets and paint strainers. Bullfrog egg masses were easily identified and distinguished from other amphibians in the region due to the large size of the gelatinous mats produced by bullfrogs at the surface of the water.

2.3. Northwestern pond turtle monitoring

We set traps to capture and monitor pond turtles at all four sites during spring and summer months (typically May–October) 2016–2021, with additional monitoring and hand captures in 2022 during continued bullfrog eradication effort. As with bullfrog eradication effort, and due to the remote location of the sites and aforementioned challenges, our effort at the four sites varied annually. We captured pond turtles using modified crab traps made of black, synthetic mesh stretched over a collapsible, metal frame partially placed above the water surface to allow access to air. For deep water placement, traps were outfitted with mesh towers affixed to the top to ensure pond turtles could surface to breathe. Traps were baited with canned mackerel and rebaited every other day. We deployed traps up to six nights at a time and checked them every 8–12 h to ensure turtle safety and maximize the effectiveness of capture. We recorded the sex of each captured pond turtle and measured the midline straight carapace length (MCL), carapace width, midline straight plastron length, plastron width, and shell height of each using field calipers. We recorded whether female pond turtles were gravid via palpation of their inguinal region. We recorded the mass (g) of each pond turtle using portable electronic scales. Counting scute annuli can be useful for aging juvenile turtles while they are young and growing quickly (Bury and Germano, 1998); the method is not reliable, however, for determining the age of adult turtles as their growth slows and scute annuli become crowded, indistinguishable, and worn smooth by weathering over time. For this reason, we used MCL in analyses to make inferences about age structure of the populations given that turtles tend to increase in size as they age (i.e., larger turtles are generally older than smaller turtles where climate and environment are similar; Congdon et al., 2013). For general comparisons, we divided pond turtles using MCL and annuli into three possible life stages: pond turtles with less than one annuli were recorded as hatchlings, pond turtles with more than one annuli (i.e., older than one year) but <110 mm in MCL were recorded as juveniles, and pond turtles >110 mm in MCL regardless of age structure or if age structure could not be determined (e.g. worn age rings) were recorded as adults. Secondary sex characteristics tend to arise around 110 mm in MCL (Bury et al., 2012). We marked each pond turtle with a unique ID by notching the marginal scutes (Cagle, 1939), following a unique numbering system (Holland, 1994). Some hatchlings <40 mm were not able to be notched; thus were photographed for later identification.

2.4. Statistical analyses

We estimated abundance and demographic rates of Northwestern pond turtles at each site with a Bayesian analysis of the Schwarz-Arnason superpopulation parameterization of the Jolly-Seber model using parameter-expanded data augmentation (Jolly, 1965; Kéry and Schaub, 2012; Schwarz and Arnason, 1996; Seber, 1965). We shared parameters across populations for efficiency and to allow estimation of quantities that otherwise would not be estimable for each population individually. Specifically, we assumed annual apparent survival was constant across years and sites, and we adjusted apparent survival in the model for the interval between sampling occasions at each site. Individual capture probability per trap check was assumed constant across sites and years. Entry probabilities were independent at each sampling occasion for each site to avoid constraining abundance estimates. In addition to apparent survival, entry, and capture probabilities, we also estimated pond turtle abundance in each sampling year and total pond turtle abundance at each site for the study period. We further calculated pond turtle densities for each site by dividing the abundance estimate for each posterior sample from the MCMC output by pond area. We assessed goodness-of-fit using the posterior predictive distribution of the number of captures of each pond turtle based on the Freeman-Tukey statistic (Rose et al., 2022), with fit for each site evaluated independently. We selected priors for each parameter to be vague and ensured that our augmented data set was not constraining abundance estimates by verifying posterior inclusion probabilities for each site were < <1.00. We fitted the model using JAGS 4.3.0 (Plummer, 2017) in R 4.3.1 (R Core Team, 2023) using the package ‘jagsUI’ (Kellner, 2015). We ran the model for 200,000 iterations on each of 5 independent chains after a burn-in period of 20,000 iterations and thinned the output by a factor of 10. We assessed convergence with examination of history plots and the Gelman-Rubin statistic (Gelman and Rubin, 1992); all history plots appeared well-mixed and $\widehat{R} < 1.01$ for all parameters of interest. Minimum effective sample size for monitored parameters was 1719.

We used linear mixed effects models to compare pond turtle size among the sites. Because bullfrogs were almost completely eradicated at the bullfrog present sites by 2020, we compared pond turtles captured from bullfrog present sites through 2019—while the pond turtles were still living with dense bullfrog populations—with those captured at the bullfrog absent sites across all years. For each model, we used MCL or mass of each pond turtle at first capture as our response variable, bullfrog presence as a fixed effect, and site as a random intercept. We performed one analysis on pond turtles of all sizes and a second analysis on just adult pond turtles (>110 mm MCL). We likewise used linear mixed effects models to compare mass (relative to length) of pond turtles among the sites, with $\log_{10}$mass at first capture as our response variable, both $\log_{10}$MCL and bullfrog presence as fixed effects, and site as a random effect. We again used a separate model for pond turtles of all sizes and for just adult pond turtles when comparing relative mass. We used the ‘lme4’ package (Bates et al., 2015) to conduct analyses in R version 4.3.1 (R Core Team, 2023). We used Kruskal-Wallis rank sum tests with a Dunn's post-hoc test of multiple comparisons where overall models were significant at the $\alpha = 0.05$ level.

3. Results

From 2015 to 2022, we recorded a total of 977 h of American bullfrog removal effort at Bullfrog Present 1 and 941 h at Bullfrog Present 2. Much of this effort was centered during 2017–2019, by which point we found the greatest success removing bullfrogs using pole spears or direct hand captures, both from boats and walking the waterbody perimeter. In total, we removed 12,317 American bullfrogs from Bullfrog Present 1 (120 egg masses, 108 larvae, 10,775 juveniles, and 1314 adults) and 4067 American bullfrogs from Bullfrog Present 2 (42 egg masses, 215 larvae, 2775 juveniles, and 1035 adults).

The number of bullfrogs removed from Bullfrog Present 1 peaked in 2018, with 6998 individuals removed that year, excluding egg masses (Fig. 1). The number of bullfrogs removed from Bullfrog Present 2 peaked in 2019, with 1822 individuals removed that year, excluding egg masses (Fig. 1). Most American bullfrogs were removed within the first five years (98.5 % from Bullfrog Present 1 and 89.1 % from Bullfrog Present 2; Fig. 1). Due to the Covid-19 pandemic and workforce limitations in 2020, only one night of bullfrog removal occurred at Bullfrog Present 1, and two nights at Bullfrog Present 2 in 2020. Despite this unexpected pause in removal effort, eradication appeared nearly complete by the end of 2019 given the lack of captures in 2020, and despite renewed, substantial effort in 2021 and 2022.

We found many prey items in bullfrog stomachs, including pond turtles (*A. marmorata*, $N = 6$), Sierra newts (*Taricha sierrae*, N = 2), garter snakes (*Thamnophis* spp., $N = 19$), frogs (*Rana catesbeiana*, $N = 60$; *Pseudacris regilla*, N = 7), Virile crayfish (*Faxonius virilis*, $N = 72$), insects ($N = 902$), unidentifiable species of small birds ($N = 7$), small rodents (N = 7), and rocks ($N = 2$). Some stomach contents were partially digested and could not be confirmed, so these numbers likely

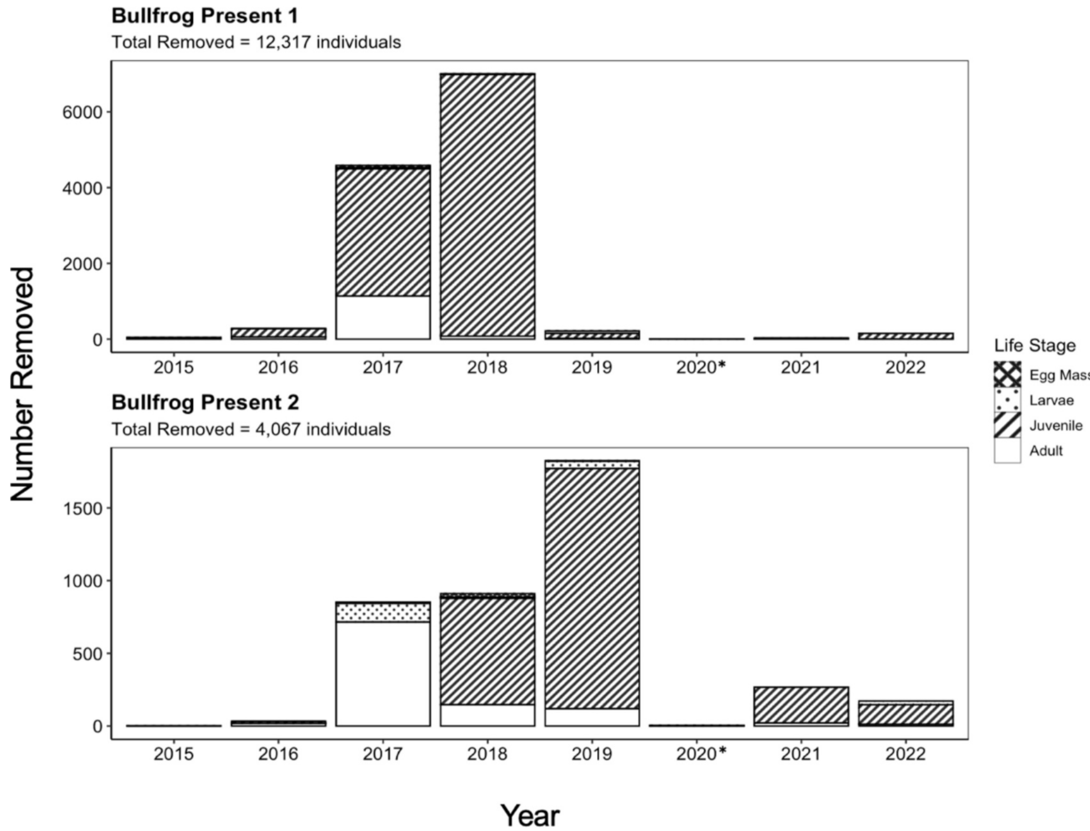

Fig. 1. Number of American bullfrogs (*Rana catesbeiana*) removed per year by life stage for both sites where bullfrogs were historically present. *Year 2020 had very limited removal effort.

underestimate true counts. All six of the pond turtles in bullfrog stomachs were hatchlings or juveniles, including four at Bullfrog Present 1 and two at Bullfrog Present 2. Two of the pond turtles found in bullfrog stomachs at Bullfrog Present 1 were found in 2021, after nearly all bullfrogs had been removed from the sites and very few remained.

We captured 45 individual pond turtles (94 total captures) at Bullfrog Present 1 and 21 individual pond turtles (24 total captures) at Bullfrog Present 2 (Table 1). We captured 222 individual pond turtles (302 total captures) at Bullfrog Absent 1 and 71 individual pond turtles (77 total captures) at Bullfrog Absent 2 (Table 1). Most captures of new individuals occurred in the first one to two years of sampling at the bullfrog present sites, whereas new individuals were still captured in later years of sampling at the bullfrog absent sites (Suppl. Fig. 1).

The Schwarz-Arnason superpopulation model sharing capture and survival information across sites generally fit the data well, with some evidence for lack of fit at Bullfrog Absent 2 (Table 2). Bullfrog absent sites were on average smaller in size yet supported higher annual pond turtle abundance estimates than sites with bullfrogs (median estimates at sites with bullfrogs, range = 22–50; sites without bullfrogs, range = 174–245; Table 2; Fig. 2). Mean pond turtle densities followed a similar pattern, being higher in the Bullfrog Absent sites than in the Bullfrog Present sites (mean estimates at sites with bullfrogs = 12 (11–14); sites without bullfrogs = 218 (182–262)). Given the mean size of the pond turtles in their respective sites, this translated to a range of 2.4–135 kg/ha of median estimated biomass, with the highest estimated pond turtle biomass occurring at one of the Bullfrog Absent sites and the lowest at one of the Bullfrog Present sites. Superpopulation estimates were similar to annual estimates (Table 2), indicating that adult pond turtle populations varied little and were generally well-sampled over the course of our study. Annual apparent survival of adult pond turtles was 0.998 (0.989–0.999; Table 2). Individual capture probability at each trap check was 0.055 (0.050–0.060; Table 2).

Pond turtle populations at the two bullfrog present sites were dominated by larger adult pond turtles (Fig. 3). In contrast, pond turtles of all sizes were captured at the bullfrog absent sites, including hatchling and juvenile pond turtles (Fig. 3). Turtles <110 mm MCL (i.e., juvenile size) on first capture represented 35.1 % of turtles at Bullfrog Absent 1, and 19.5 % at Bullfrog Absent 2. No hatchling or juvenile pond turtles were ever captured in traps at Bullfrog Present 1; the only hatchling or juvenile pond turtles recovered from Bullfrog Present 1 were four removed from bullfrog stomachs. Just one hatchling and one juvenile were captured in traps at Bullfrog Present 2, both captured after bullfrogs were nearly completely eradicated in 2019 (Fig. 3).

The lack of smaller pond turtles at the bullfrog present sites through 2019 was conspicuous, with pond turtles captured at the bullfrog present sites through 2019 being 26–35.5 % larger by MCL on average than

Table 1
Lake size, number of individual pond turtles captured, the total number of times they were captured, the median estimated population size (95 % credible intervals), and the estimated population density using estimated population sizes for each study site in Yosemite National Park from 2016 to 2022. For bullfrog present sites, mean midline carapace length (± standard deviation), mean mass (± standard deviation), and estimated biomass density of Northwestern pond turtles (*Actinemys marmorata*) represent pond turtles captured before near complete eradication of bullfrogs (through 2019). For bullfrog absent sites, the measurements represent pond turtles from all years (2016–2022).

Site name	Lake size (ha)	Individuals captured	Total captures	Estimated population size	Estimated density (turtles/ha)	Mean MCL (mm)	Mean mass (g)	Estimated biomass density (kg/ha)
Bullfrog Present 1	2.5	45	94	50 (46–58)	20.2 (18.4–23.2)	166.9 (±8.8)	648.2 (±85.7)	13.1 (11.9–15.0)
Bullfrog Present 2	7.8	21	24	31 (24–43)	4.0 (3.1–5.5)	162.9 (±12.3)	598.8 (±107.7)	2.4 (1.8–3.3)
Bullfrog Absent 1	5.78	222	302	246 (234–264)	42.6 (40.3–45.5)	123.2 (±34.9)	329.5 (±204.5)	14.1 (13.3–15.0)
Bullfrog Absent 2	0.5	71	77	198 (162–242)	395.5 (322–480)	129.3 (±27.5)	340.9 (±169.7)	135 (110–164)

those captured at the bullfrog absent sites throughout the study ($p = 0.002$; Fig. 3; Table 1). Pond turtles did not differ significantly in MCL between Bullfrog Present 1 and 2 ($p = 0.60$) or between Bullfrog Absent 1 and 2 ($p = 0.85$). Among just adult pond turtles, those captured at the bullfrog present sites through 2019 were 11.8–19 % larger by MCL on average than those captured at the bullfrog absent sites throughout the study ($p = 0.017$; Fig. 4). Adult pond turtles did not differ significantly in MCL between Bullfrog Present 1 and 2 ($p = 0.48$) but were larger at both bullfrog present sites than at Bullfrog Absent 1 (p-values < 0.0001), where they were in turn larger than at Bullfrog Absent 2 ($p = 0.018$; Fig. 4). Mass followed a similar trend due to the lack of smaller pond turtles—pond turtles captured at bullfrog present sites through 2019 were 75.7–96.7 % heavier on average than pond turtles captured at bullfrog absent sites throughout the study ($p < 0.0001$; Table 1). Pond turtles did not differ significantly in mass between Bullfrog Present 1 and 2 ($p = 0.45$) or between Bullfrog Absent 1 and 2 ($p = 0.98$). Among just adult pond turtles, those captured at the bullfrog present sites through 2019 were 31.4–62 % heavier on average than adults captured at bullfrog absent sites throughout the study ($p = 0.031$, data not shown). As with MCL, adult pond turtles did not differ significantly in mass between Bullfrog Present 1 and 2 ($p = 0.31$) but were heavier at both bullfrog present sites than Bullfrog Absent 1 (p-values<0.001), where adult pond turtles were in turn heavier than Bullfrog Absent 2 ($p = 0.007$). The relative mass of pond turtles at bullfrog present sites through 2019 did not differ from those captured at the bullfrog absent sites throughout the study ($p = 0.96$). Likewise, among just adult pond turtles, the relative mass of those captured at the bullfrog present sites through 2019 did not differ from those captured at the bullfrog absent sites throughout the study ($p = 0.48$).

4. Discussion

The American bullfrog is included among the world's 100 worst invasive species due to its impact on native biodiversity (Lowe et al., 2000). Its wide ecological niche means that native freshwater species including freshwater turtles—a group already imperiled globally (Dudgeon et al., 2006)—are often at particular risk where bullfrogs are established. While the challenges presented by invasive bullfrogs are diverse, it is their opportunistic and generalist nature as predators that often gives them an outsized impact on native species (Moyle, 1973; Bury and Whelan, 1984; Pearl et al., 2004; Jancowski and Orchard, 2013). This risk is heightened for species like turtles, whose populations are slow to respond even when conservation threats are alleviated (Gibbons et al., 2000; Enneson and Litzgus, 2008).

As opportunistic predators, bullfrogs are gape-limited in prey choice (Carpenter and Morrison, 1973), and adult pond turtles are simply too large to be consumed by bullfrogs. However, the opposite is true for hatchlings and other young pond turtles. Among the varied prey items we found in bullfrog stomachs at the two study sites were six separate instances of small pond turtles. This likely underrepresents the true number of pond turtles consumed by bullfrogs given that one instance of a pond turtle in the stomach contents was mostly digested (e.g., only one hatchling limb and one scute fragment evident in one stomach), and the odds of capturing a bullfrog that had fed recently enough for the entire turtle to still be identifiable was likely low. For comparison, in a study from British Columbia, Canada, 12 native Western painted turtle hatchlings were found in bullfrog stomachs in just six months (Jancowski and Orchard, 2013). Our detections now join a growing list of observations of bullfrogs preying on small pond turtles where bullfrogs were introduced (Korschgen and Baskett, 1963; Hothem et al., 2009; Hallock et al., 2017; Nicholson et al., 2020). Given that hatchling pond turtles can measure as little as 25 mm in MCL, they likely take several years to outgrow the gape of an adult bullfrog (Bury et al., 2012) and remain at risk of predation by bullfrogs. Prolonged predation risk coupled with slow maturation rates (7–10 years), limited reproductive rates (e.g., typically 4–6 eggs per nest), and high nest depredation means

Table 2
Prior and posterior distributions for Schwarz-Arnason superpopulation parameterization of the Jolly-Seber model to estimate site- and year-specific abundance of Northwestern pond turtles (*Actinemys marmorata*) captured in turtle traps in Yosemite National Park, California, USA, 2016–2021. SD = standard deviation, ETI = equal-tailed interval. *Beta*(α, β) indicates a prior with a beta distribution and two shape parameters (α and β). Note entry probabilities were given a Dirichlet prior as specified in Kéry and Schaub (2012). The Gelman-Rubin convergence diagnostic ($\widehat{R}$) was 1.00 for all reported values in the table and the minimum effective sample size across all parameters was 2243.

Parameter	Site	Symbol	Prior	Posterior distribution summary		
				Mean ± SD	Median	95 % ETI
Inclusion probability	Bullfrog Absent 1	ψ_{BA1}	*Beta*($\alpha = 1$, $\beta = 1$)	0.49 ± 0.03	0.49	0.44–0.55
	Bullfrog Absent 2	ψ_{BA2}	*Beta*(1, 1)	0.40 ± 0.05	0.40	0.31–0.50
	Bullfrog Present 1	ψ_{BP1}	*Beta*(1, 1)	0.34 ± 0.04	0.34	0.26–0.43
	Bullfrog Present 2	ψ_{BP2}	*Beta*(1, 1)	0.32 ± 0.07	0.31	0.20–0.47
Annual apparent survival probability	Shared across sites and years	ϕ	*Beta*(1, 1)	0.997 ± 0.003	0.998	0.989–1
Mean capture probability per trap-check	Shared across sites and years	p	*Beta*(1, 1)	0.055 ± 0.002	0.055	0.05–0.06
Abundance	Bullfrog Absent 1 in 2018	N_{BA1_2018}	Derived parameter	174.11 ± 12.49	174	151–200
	Bullfrog Absent 1 in 2019	N_{BA1_2019}	Derived parameter	230.76 ± 7.33	231	217–245
	Bullfrog Absent 1 in 2020	N_{BA1_2020}	Derived parameter	245.25 ± 7.47	245	232–261
	Bullfrog Absent 1 in 2021	N_{BA1_2021}	Derived parameter	245.78 ± 7.76	245	232–263
	Bullfrog Absent 2 in 2018	N_{BA2_2018}	Derived parameter	190.51 ± 20.21	189	154–233
	Bullfrog Absent 2 in 2021	N_{BA2_2021}	Derived parameter	197.01 ± 20.42	196	160–240
	Bullfrog Present 1 in 2018	N_{BP1_2018}	Derived parameter	45.27 ± 3.22	46	38–51
	Bullfrog Present 1 in 2019	N_{BP1_2019}	Derived parameter	48.66 ± 2.06	48	45–53
	Bullfrog Present 1 in 2021	N_{BP1_2021}	Derived parameter	50.18 ± 3.12	50	46–58
	Bullfrog Present 2 in 2016	N_{BP2_2016}	Derived parameter	22.12 ± 3.54	22	16–29
	Bullfrog Present 2 in 2018	N_{BP2_2018}	Derived parameter	27.92 ± 3.66	27	22–36
	Bullfrog Present 2 in 2019	N_{BP2_2019}	Derived parameter	29.31 ± 4.17	29	23–39
	Bullfrog Present 2 in 2021	N_{BP2_2021}	Derived parameter	31.32 ± 5.08	31	23–43
Superpopulation abundance	Bullfrog Absent 1	N_{super_BA1}	Derived parameter	246.94 ± 7.75	246	234–264
	Bullfrog Absent 2	N_{super_BA2}	Derived parameter	198.84 ± 20.58	198	162–242
	Bullfrog Present 1	N_{super_BP1}	Derived parameter	50.42 ± 3.11	50	46–58
	Bullfrog Present 1	N_{super_BP2}	Derived parameter	31.56 ± 5.10	31	24–43
Bayesian *P*-value	Bullfrog Absent 1		Derived parameter	0.88 ± 0.32	1	0–1
	Bullfrog Absent 2		Derived parameter	0.06 ± 0.23	0	0–1
	Bullfrog Present 1		Derived parameter	0.32 ± 0.47	0	0–1
	Bullfrog Present 2		Derived parameter	0.46 ± 0.50	0	0–1

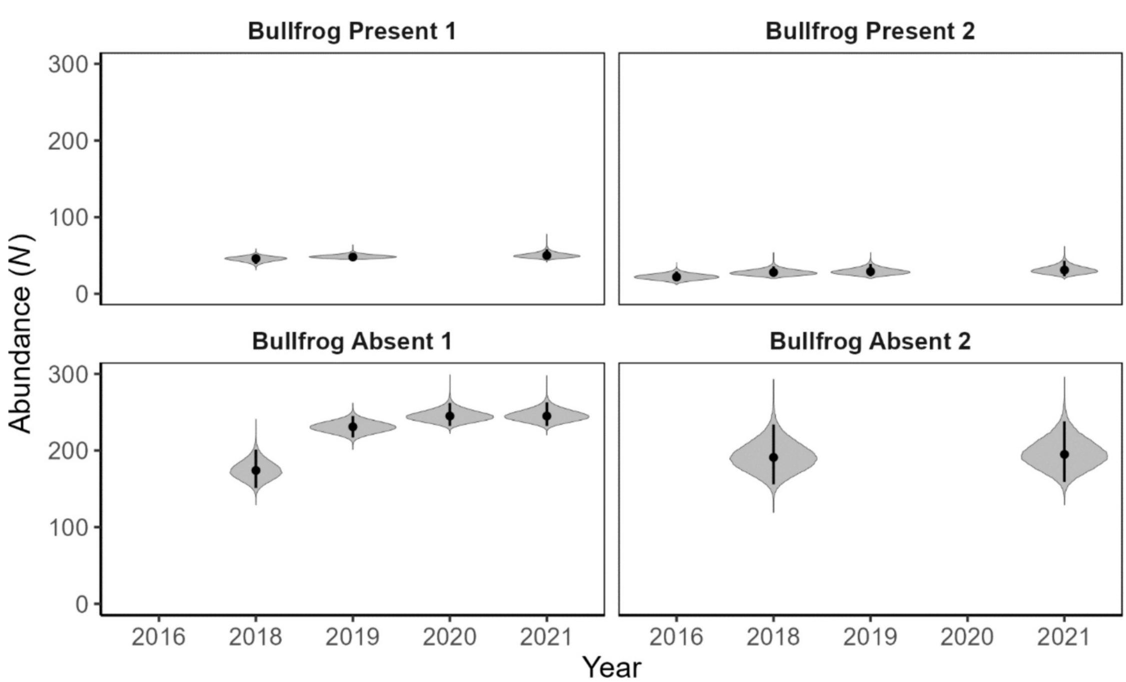

Fig. 2. Annual abundance estimates for Northwestern pond turtles (*Actinemys marmorata*) captured in turtle traps by site and year for sites with (upper panels) and without (lower panels) American bullfrogs (*Rana catesbeiana*). Bullfrog removal occurred from 2016 to 2022 at Bullfrog Present 1 and 2. Points represent posterior medians, vertical lines represent 95 % equal-tailed intervals, and shapes represent posterior distributions.

that few turtles are likely to survive to sexual maturity (Holland, 1994; Bury et al., 2012), placing this long-lived species at particular risk. Our study adds mounting evidence that hatchling and juvenile pond turtle losses to bullfrogs pose a serious threat to pond turtle population persistence. The impact of bullfrogs on pond turtles was even listed as one cause for the proposed listing of the turtle as threatened under the Endangered Species Act (USFWS, 2023).

An obvious consequence of consistent and prolonged predation of

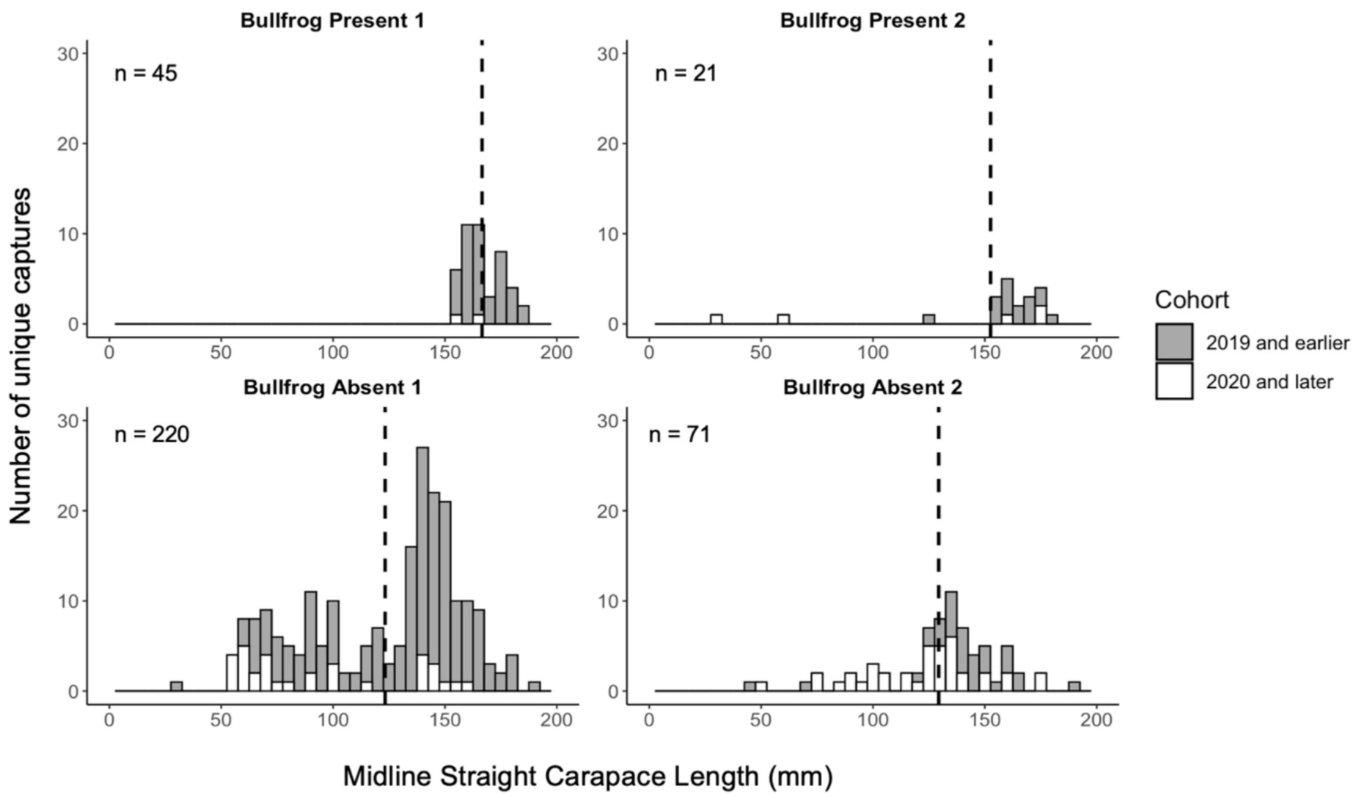

Fig. 3. Size frequency histograms of Northwestern pond turtles (*Actinemys marmorata*) upon first capture. American bullfrog removal occurred at Bullfrog Present 1 and 2 from 2016 to 2022. Bullfrog Absent 1 and 2 had no bullfrog presence. Gray bars represent pond turtles captured in 2019 or earlier, and white bars represent pond turtles captured in 2020 and later after reaching near complete bullfrog eradication. Vertical black dashed lines depict the mean midline straight carapace length for each site across all years. Sample size of individual pond turtles is in the upper left corner of each site's panel.

young pond turtles by American bullfrogs is the lingering demographic impact observed in our study. At the sites where bullfrogs were present, pond turtles had low population densities and were dominated by larger individuals, which would be consistent with an aging population that is demographically top heavy. Such effects in pond turtle populations have previously been attributed to prolonged cohabitation with bullfrogs (Holland, 1991; Sloan, 2012; Nicholson et al., 2020). While adult pond turtles in these populations were still reproducing—evidenced by the appearance of hatchlings in bullfrog stomachs—sustained predation by bullfrogs meant no pond turtles survived long enough to be recruited into later life-stages. Extremely truncated populations composed of just adult turtles indicates a declining population that, if unmitigated, will lead to local extinction (Browne and Hecnar, 2007; Howell et al., 2019). Without the active bullfrog eradication undertaken here, these turtle populations are unlikely to have recovered on their own. Our study shows that control efforts in the short-term are likely to benefit pond turtle populations until long-term solutions (e.g. full eradication) can be reached. Unfortunately, declines in turtle populations can happen surreptitiously as adults persist for decades due to long lifespans and high survival while no juveniles survive to replace them. This phenomenon, coined the "perception of persistence", can provide a false sense of security and delay management intervention necessary for species conservation (Lovich et al., 2018). In the case of mitigating American bullfrog impacts to pond turtle populations, this management intervention may need to take the form of protracted effort to remove invasive bullfrogs altogether.

Our results suggest that sustained, direct removal of bullfrogs, while demanding, can succeed in dramatically reducing populations and predation pressure on native species. Study sites containing bullfrogs escaped management attention for decades, allowing populations to grow and reach high densities. The number of bullfrogs removed from the 2.5-ha Bullfrog Present 1 far surpassed even the highest numbers reported from other studies for a single population. Louette et al. (2012) targeted primarily tadpoles but removed 9212 individuals from a 0.15-ha pond over two years. In another region of Yosemite National Park, park staff removed 8126 individuals over 15 years from the Yosemite Valley—a region that spans approximately 1500 ha (Kamoroff et al., 2020). Using a conservative estimate of 25 g of body mass per bullfrog, we estimate that we removed >300 kg of bullfrog biomass over the eight years from Bullfrog Present 1 alone. The bullfrog biomass removed from the study sites here represents substantial energy being redirected to bullfrogs and away from native species. We know from historical park records, for instance, that California red-legged frogs (*Rana draytonii*) were widespread in this region prior to bullfrog introduction (Adams et al., 2023a). Following near eradication of bullfrogs at Bullfrog Present 2, we recorded the first captures of small pond turtles—a hatchling and a juvenile—suggesting a strong relationship between bullfrog removal and pond turtle recruitment and thus providing some hope for turtle population recovery once bullfrog predation pressures are alleviated. The sustained pressure from bullfrogs likely plays a sizeable role in low pond turtle recruitment and the slow decline of wild pond turtle populations where the two species cohabitate. Any attempt to reverse range-wide declines of pond turtles in the western US may thus benefit from including bullfrog control.

Studies continue to show that the successful removal of invasive species can support native species recovery (Genovesi, 2005; McGeoch et al., 2010). The eradication of bullfrogs from Yosemite Valley (Kamoroff et al., 2020) prompted the facilitated reintroduction of California red-legged frogs (*Rana draytonii*) using captive-reared populations that have since shown signs of wild reproduction and recruitment (Adams et al., 2023b). Similarly, after mountain yellow-legged frogs (*Rana sierrae* and *R. muscosa*) disappeared from 90 % of their historical California range, the removal of non-native trout from remote alpine lakes resulted in the rapid increase of native frog densities

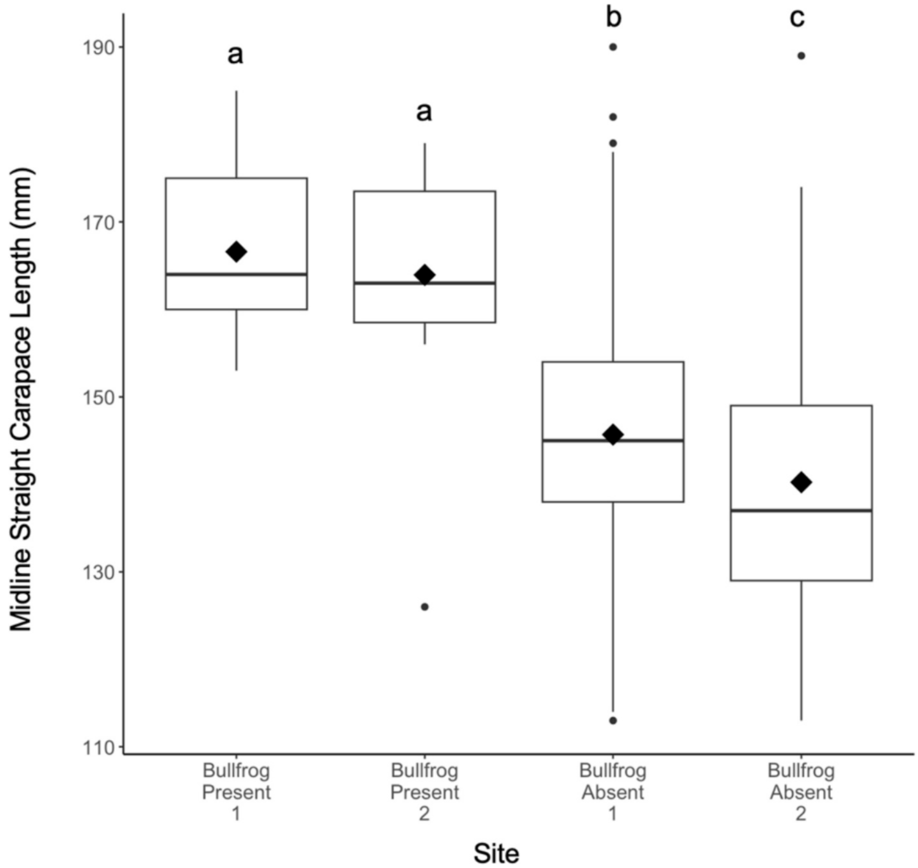

Fig. 4. Box and whisker plots of midline straight carapace length (MCL) of Northwestern pond turtles (*Actinemys marmorata*) at each site using only reproductive, adult pond turtles (>110 mm MCL) upon their first capture. Means are depicted by black diamonds. Boxes indicate the interquartile range of each site's distribution of values (i.e., the upper and lower box boundaries correspond to the 25th to the 75th percentiles); within each box, the middle horizontal line denotes the median. Vertical whisker lines extend 1.5 times the interquartile range from the top and bottom of each box, excluding outliers shown as points. Note the y-axis begins at 110 mm. Lowercase letters above boxplots denote post-hoc comparisons evaluated at $\alpha = 0.05$.

(Vredenburg, 2004; Knapp et al., 2007). Our efforts to dramatically reduce bullfrog abundances have supported the reintroduction of the California red-legged frog in this region. Our work underscores the considerable time, effort, and dedication required to remove bullfrogs and monitor the effects on native turtle populations long-term. To prevent bullfrog populations from rebounding, continued removal on the bullfrogs that remain will be essential for pond turtles and other native species to recover. While our study examined the detrimental effect of invasive bullfrogs on a declining native turtle species of concern, the implications for freshwater systems are broad in the face of increasingly altered environments. Given the wide range of negative effects bullfrogs can have on freshwater systems, early detection and proactive bullfrog management can have multi-species benefits and be a worthwhile endeavor for restoring freshwater ecosystems.

5. Conclusion

Invasive species are among the greatest threats to biodiversity with potential to cause permanent damage to native ecosystems (Blackburn et al., 2019). American bullfrogs represent one example of a globally distributed invasive species that has been implicated in the decline of many native freshwater species (Lowe et al., 2000). Our study investigated how prolonged American bullfrog presence affected Northwestern pond turtle demographics while simultaneously assessing the efficacy of targeted bullfrog removal aimed at ameliorating these effects. We found prolonged bullfrog predation on small pond turtles likely inhibited pond turtle recruitment, evidenced by the low population densities and demographically "top-heavy" structure we observed in pond turtle populations at bullfrog present sites. However, our targeted removal of adult and juvenile bullfrogs coincided with the first observations of young pond turtles at our bullfrog present sites, indicating that bullfrog removal may facilitate population recovery for native pond turtles. While the challenges associated with invasive species removal are significant, our study shows the potential benefit of reversing species declines and restoring freshwater ecosystems.

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Permits and protocols

Work was conducted under an approved California Department of Fish and Wildlife Scientific Collecting Permit (SC-5130), NPS IACUC protocol, and NPS-YOSE Permits: YOSE-2016-SCI-2016-0101, YOSE-2017-SCI-0098, YOSE-2018-SCI-0072, YOSE-2019-SCI-0029, YOSE-2020-SCI-0038, YOSE-2021-SCI-0075, and YOSE-2022-SCI-0048.

CRediT authorship contribution statement

Sidney M. Woodruff: Writing – review & editing, Writing – original draft, Visualization, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization. **Robert L. Grasso:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization. **Brian J. Halstead:** Writing – review & editing, Visualization, Formal analysis. **Brian D. Todd:** Writing – review & editing, Writing – original draft, Supervision, Project administration, Formal analysis, Conceptualization.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this article.

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Any use of trade, product, website, or firm names in this publication is for descriptive purposes only and does not imply endorsement by the U.S. Government.

Data availability

Due to the sensitive nature of this imperiled species and its proposed protected status, raw data and locations are not provided.

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