Chapter thirty-eight

Problems and opportunities managing invasive Bullfrogs: is there any hope?

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INTRODUCTION

The American Bullfrog (*Rana catesbeiana* Shaw) is a widely introduced and invasive anuran that is frequently blamed for population declines of indigenous species (Bury and Whelan 1984). Once established, Bullfrog populations are often either difficult or impossible to eradicate depending on habitat and landscape features (Schwalbe and Rosen 1988, Doubledee *et al*. 2003, Govindarajulu *et al*. 2005). Bullfrogs are representative of a large but neglected suite of non-indigenous species (NIS) that are characterized by: (1) a broad invasion that is well established in some areas; (2) a lack of obvious economic impacts compared to some other invasive species; and (3) a lack of reasonably feasible control methods. Despite demonstrated conservation concerns, invasive species like the Bullfrog do not tend to attract the resources necessary to attempt large scale management because of their lack of economic impact and the difficulty of control methods. This leaves biologists responsible for managing habitats invaded by such species with little hope and few options for promoting the persistence of sensitive indigenous species. With these issues in mind, we consider the case of the Bullfrog, review management options, and suggest directions for future research with this and similar species.

Bullfrogs are among the most successful vertebrate invaders and are considered by the IUCN Invasive Species Specialist Group to be among the 100 worst invaders in the world (http://www.issg.org/database/welcome). The

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native range of the Bullfrog covers much of eastern North America, roughly from the Mississippi River and Great Lakes east to the Atlantic Ocean and from the State of Florida north into southern Canada (Bury and Whelan 1984). Few anurans exhibit such a large native range. This broad native distribution is indicative of the adaptability and success of Bullfrogs and is dwarfed by their present range. They now occupy much of the western USA (Casper and Hendricks 2005), and parts of western Canada (Green and Campbell 1984), Mexico (Casas-Andreu *et al.* 2002), Brazil (Borges-Martins *et al.* 2002), Ecuador (Cisneros-Heredia 2004), Venezuela (Hanselmann *et al.* 2004), Cuba (Sampedro *et al.* 1985), Dominican Republic (Kairo *et al.* 2003), Jamaica (Mahon and Aiken 1977), Puerto Rico (Lopez-Flores *et al.* 2003), Hawaii (Viernes 1995), Japan (Hirai 2004), China (Wu *et al.* 2004), Korea (Kim and Ko 1998), Italy (Lanza 1962), France (Neveu 1997), the Netherlands (Stumpel 1992), and the UK (Banks *et al.* 2000), among other locations (Lever 2003).

Original introduction of Bullfrogs to many of these locations occurred more than 50 years ago for culturing as a food source, sometimes after the overharvest of indigenous anurans (Jennings and Hayes 1985, Negroni 1997, Mazzoni 1999). Escapees and intentional releases established naturalised populations that are often difficult to eradicate. Post-metamorphic stages are capable of dispersing long distances and are adept at colonizing new sites (>1200 m; Willis *et al.* 1956). A single female Bullfrog can produce 1,000–25,000 eggs with the largest females sometimes producing more than 40,000 eggs (Bury and Whelan 1984). Breeding sites can achieve notably high densities (>780 adults ha^{-1}; Schwalbe and Rosen 1988).

The conspicuousness (e.g. large size, high densities, and loud vocalizations) and natural history (e.g. high fecundity and broad diet) of Bullfrogs make their introduction an obvious hypothesis to explain declines in indigenous species. Early reports suggested displacement of indigenous amphibians (Moyle 1973, Hammerson 1982), but separating the influence of Bullfrogs from correlated factors has proven difficult (Hayes and Jennings 1986, Adams 1999). Some studies suggest that other factors associated with Bullfrog presence, like introduced fish or habitat alterations, may be more detrimental to indigenous species than the Bullfrogs themselves (Kiesecker and Blaustein 1998, Adams 1999, 2000). However, an increasing number of studies shows direct and indirect negative effects of Bullfrogs on indigenous anurans via competition, predation, and habitat displacement (Boone *et al.* 2004, Pearl *et al.* 2004, others reviewed in Kiesecker 2003). Bullfrog invasions may also affect other taxa such as aquatic snakes and waterfowl (Viernes 1995, Rosen and Schwalbe 2002, Lopez-Flores and Vilella 2003, Wylie *et al.* 2003). Recent work raises the possibility that Bullfrogs may serve as a reservoir of a chytrid fungus, *Batrachochytrium dendrobatidis* (Longcore *et al.* 1999), pathogenic to some amphibians (Hanselmann *et al.* 2004, Pearl and Green 2005, Garner *et al.* 2006). Despite some conflicting reports and regional differences in effects, Bullfrogs are clearly a conservation concern.

MANAGEMENT OPTIONS

Ongoing expansion of Bullfrogs to a wide variety of regions and habitats underscores the need for a suite of management approaches. No discussion of management options for invasive species is complete without mentioning prevention. The best way to control invasive species is to prevent their introduction or establishment in new regions. This is because it is often difficult to detect new invasions early and eradication is much more realistic for species with a limited distribution (Simberloff *et al.* 2005). A review of the papers cited in our introduction on the geographic extent of the Bullfrog invasion suggests that most Bullfrog introductions have been associated with aquaculture. Escape from such operations appears impossible to stop completely. Other vectors include the use of Bullfrog tadpoles as bait for recreational fishing and the availability of live Bullfrogs for pets, landscape ponds, research, and teaching. Efforts to reduce or eliminate these vectors are warranted to slow or prevent the spread of Bullfrogs, but we will not attempt a detailed analysis of such prevention options here. Instead, we focus on methods applicable to established populations.

Direct removal

We define direct removal of Bullfrogs as actions that have a proximate result of death or removal of Bullfrog individuals from the wild. This is in contrast to other options described below that seek to reduce the survival or effects of Bullfrogs by manipulating aspects of their environment. There are a few anecdotal accounts of efforts to directly control Bullfrogs but we are not aware of any publications that fully detail such efforts. Banks *et al.* (2000) installed fencing around the main ponds to limit dispersal and used lamps to collect adult frogs at dusk. They then drained the ponds and excavated the sediment to remove remaining frogs and larvae. This effort apparently did not result in complete eradication: limited breeding was detected the following summer, and post metamorphic bullfrogs were found in the vicinity two years after management (B. Banks 2006, personal communication). Another direct removal effort that has been partially documented in the literature is in ponds that are relatively isolated in a desert landscape in Arizona, USA (Schwalbe and Rosen 1988, Rosen and Schwalbe 1995). They used funnel traps, gigs, guns, and hand capture to remove Bullfrogs annually. Reductions in Bullfrog densities were said to be small and short-lived.

Direct removal techniques are hampered by strong density dependence. Bullfrog populations may exhibit density dependence in both the larval and post-metamorphic segments of their life history (Doubledee *et al.* 2003, Govindarajulu *et al.* 2005). Demographic perturbation analyses of data from invaded ponds in British Columbia suggest that removal efforts should target juveniles and tadpoles that transform after one instead of two winters (Govindarajulu *et al.* 2005). This is consistent with elasticity analyses for other pond-breeding anurans that predict that reducing survival of juveniles rather than other life stages should have the greatest effect on population growth rate (Biek *et al.* 2002, Vonesh and de la Cruz 2002). For Bullfrogs and some other temperate ranids, incomplete removal of eggs or larvae can boost growth and survival of remaining individuals via strong density dependence (Altwegg 2002, Govindarajulu 2004). Likewise, a reduction in the density of adult Bullfrogs can increase the survival of juveniles that would otherwise be prey for adults (Werner *et al.* 1995, Doubledee *et al.* 2003, Govindarajulu 2004). Doubledee *et al.* (2003) used population models to evaluate the potential effectiveness of shooting adult Bullfrogs. Their results suggest that efforts sufficient to increase adult mortality by 65% or greater every 2 years would be necessary to reduce Bullfrog densities enough to benefit California Red-Legged Frogs (*Rana draytonii* Baird and Girard). However, they also suggest that this level of mortality would be difficult to achieve and that the resulting fluctuations in the Bullfrog population might lead to dangerous instability in the California Red-Legged Frog population. Bullfrog life history and demography vary among sites and regions (e.g. Viparina and Just 1975, Cecil and Just 1979), and this variation will need to be accounted for in control prescriptions (Govindarajulu *et al.* 2005).

The high fecundity, density dependence, and evasiveness of Bullfrogs, along with the complexity of invaded wetlands, often make direct removal difficult. Even in small and relatively simple ponds, direct manual removal may need to be coupled with other activities to eradicate or control a population (Banks *et al.* 2000, Doubledee *et al.* 2003). Still, such actions are warranted in situations where Bullfrogs are threatening an endangered species and in the early stages of invasion. Direct removal will be more effective for small, isolated ponds where removal can be complete and reinvasion by overland dispersal is less likely.

Habitat manipulation

Given that direct removal is usually difficult, finding methods to indirectly control Bullfrogs or their effects is appealing. Opportunities to manage habitats present themselves in the course of other management activities. For example, wetland creation, restoration, and enhancement projects offer the chance to manipulate wetland characteristics in ways that promote indigenous versus invasive species. Preventing or controlling invasive plants is often a goal of wetland restoration or enhancement (e.g. Kentula *et al.* 1992). The role that wetland characteristics can play in managing invasive animals like the Bullfrog is less clear.

Some authors have suggested habitat and landscape characteristics that might be managed to limit the dispersal of Bullfrogs. For example, connections to permanent ponds in the form of streams, ditches, or flooding might increase the chance that Bullfrogs will invade a site (Pearl *et al.* 2005). Among other things, this suggests that mitigation of isolated wetlands that are lost to development should emphasize isolation as a desirable characteristic for new sites created. This has intuitive appeal, but the factors that influence Bullfrog movement through a landscape require more study. Moreover, the effects of connectivity and landscape patterns on the dynamics of indigenous species must also be considered.

Habitat management can be viewed as a technique to indirectly reduce or eliminate Bullfrogs. An obvious example is the alteration of hydroperiod. Bullfrogs overwinter as larvae in many regions and they generally depend on permanent waters for larval growth. Maret *et al.* (2006) found that drying could be used to eliminate Bullfrogs in some livestock watering ponds. Pond drying was also effective for local elimination of non-indigenous fish (Maret *et al.* 2006), which can interact with Bullfrogs in ways detrimental to indigenous anurans (Kiesecker and Blaustein 1998, Adams *et al.* 2003). Model comparisons of pond drying and adult removal caused Doubledee *et al.* (2003) to conclude that draining ponds every two years might reduce Bullfrog densities enough to allow the persistence of California Red-Legged Frogs. Their models suggest that a combination of adult removal and periodic pond draining can be an effective strategy to allow coexistence of California Red-Legged Frogs with Bullfrogs.

The use of pond drying to limit Bullfrogs and benefit natives requires additional research and will be region-specific. How to use drying rotations to reduce Bullfrogs without harming natives in groups of wetlands is poorly known (e.g. Maret *et al.* 2006). Drying effects on indigenous species must be considered fully prior to implementing such management plans. A case in point is the conservation of the threatened California Red-Legged Frog, which was recently confirmed to overwinter as larvae in some sites (Fellers *et al.* 2001). In warmer portions of their range, Bullfrogs are capable of reaching transformation in their first summer (Cohen and Howard 1958, Bury and Whelan 1984). Care must be taken to time draining such that there will not be selection for rapid development of larval Bullfrogs. This means draining the pond fast enough and early enough to prevent any rapidly developing portion of the population from reaching metamorphosis.

Whether there are habitat features other than hydroperiod that can be manipulated to control Bullfrog density is an open question. There is some evidence that Bullfrogs are less abundant in ponds in the Pacific Northwest with shallow sloping banks and extensive emergent vegetation (Adams *et al.* 2003). This may have less to do with Bullfrog habitat requirements than with associated patterns in the community (see Community Characteristics below), but suggests the possibility that pond characteristics other than hydroperiod can be manipulated to limit Bullfrogs.

Habitat characteristics can also mediate the interactions between two species. For example, it has long been thought that habitat complexity can facilitate prey survival (Huffaker 1958, Crowder and Cooper 1982, Sredl and Collins 1992). Habitat diversity can decrease encounter rates by increasing habitat segregation of predator and prey (Smith 1972). Habitat segregation could serve to reduce both predation and competition (Smith 1972). Structure such as vegetation can also reduce the effectiveness of some predators by reducing encounter rates within microhabitats (Savino and Stein 1982, Babbitt and Jordan 1996). It has been argued that short term measures that favor the indigenous species might allow natives to adapt in a way that allows their long-term persistence without further intervention (Schlaepfer *et al.* 2005). For example, when exposed to chemical cues from Bullfrogs, Red-legged frogs from populations that are syntopic with Bullfrogs can exhibit behavioral defenses that are enhanced relative to allotopic populations (Kiesecker and Blaustein 1997).

The demography of the typical pond breeding anuran is such that predation by Bullfrogs on recently transformed juveniles might be particularly detrimental to indigenous populations (Biek *et al.* 2002, Vonesh and de la Cruz 2002). This suggests a hypothesis that providing some form of cover in the portion of a pond where juvenile indigenous frogs emerge could promote survival of natives by reducing Bullfrog predation on natives. It has also been suggested that providing riparian cover and feeding areas around ponds and suitable streams can encourage indigenous species to leave the pond habitats where they are more likely to encounter Bullfrogs (Govindarajulu 2004). These hypotheses illustrate that the potential use of habitat to mediate Bullfrog interactions with indigenous species warrants further study.

Despite extensive theoretical evidence that habitat characteristics could influence the probability that indigenous species can coexist with Bullfrogs, there is little information upon which to base habitat guidelines. Indeed, there is currently a need for observations that identify habitat characteristics to test. Studies that quantify associations between Bullfrogs and various indigenous species (e.g. Adams 1999, Kiesecker *et al.* 2001) provide a ready source of data to further define habitat attributes that could increase persistence of natives if Bullfrogs are not eradicated. For example, a study conducted by Pearl *et al.* (2005) in the Willamette Valley of western Oregon takes the traditional approach of evaluating the potential for Bullfrogs to exclude indigenous amphibians but could, instead, investigate predictors of coexistence between indigenous species and Bullfrogs. We revisited these data to determine whether wetlands with coexistence had habitat characteristics that differed from wetlands where only Bullfrogs or only the indigenous species (Northern Red-Legged Frog, *Rana aurora* Baird and Girard) are found. Using Principal Components Analysis, we explored the explanatory value of variables related to wetland size, vegetation, depth, height of riparian vegetation, substrate slope, and road length within 200 m. We targeted these variables because large wetlands and shallow wetlands with extensive emergent vegetation might allow greater microhabitat segregation of Bullfrogs and indigenous species. Likewise, suitable riparian characteristics might reduce the amount of time that indigenous species spend in contact with the more aquatic Bullfrogs. Our analysis indicated that wetlands with greater portions of surface area with emergent vegetation might be more likely to support coexistence or to support Northern Red-Legged Frogs alone

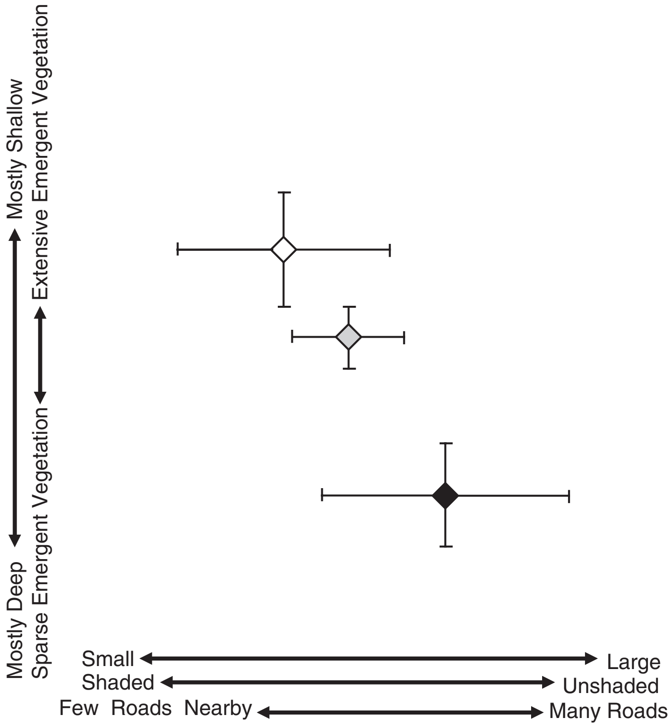

Fig. 1 Characteristics of wetlands with Northern Red-legged Frogs only (open diamond), Northern Red-legged Frogs and Bullfrogs (gray diamond), and Bullfrogs only (black diamond). The axes are principal components based on habitat variables measured during surveys for amphibians at 85 wetlands in the Willamette Valley, Oregon (Pearl *et al.* 2005).

(Fig. 1). As this was just an exploratory analysis, this pattern should be considered preliminary rather than conclusive. However, this approach can contribute to understanding coexistence by supplementing the more common approach of describing the occupancy and abundance of indigenous species relative to Bullfrog presence, Bullfrog abundance, and habitat characteristics. The pattern of coexistence in the Willamette Valley shows that further research seeking options to promote coexistence of indigenous amphibians with Bullfrogs via habitat management is warranted.

Community characteristics

Larval Bullfrogs differ from most other temperate ranids in several ecologically important ways. In their native range, Bullfrogs share permanent waters with a variety of warm water fish (Werner and McPeek 1994). In particular, Bullfrogs often co-occur with sunfish (family Centrarchidae), which include pumpkinseed, bluegill, crappie, and bass. Many fish avoid feeding on Bullfrog tadpoles which are somewhat unpalatable (Kruse and Francis 1977, Kats *et al.* 1988). These fish have an effect on pond communities that Bullfrogs exploit: they reduce the size and abundance of macroinvertebrates that can be major predators of Bullfrog larvae (Werner and McPeek 1994, Skelly 1996).

Research in the State of Oregon, USA, has shown that invasive bluegill (*Lepomis macrochirus* Rafinesque) increase the survival of Bullfrog tadpoles by reducing the abundance of indigenous aeshnid dragonfly larvae (Adams *et al.* 2003). Survival of Bullfrog tadpoles was 0% in experimental enclosures that lacked bluegill but had aeshnids; compared to 20% survival in enclosures with both bluegill and aeshnids. This suggests that reducing or eliminating bluegill and perhaps other similar centrarchids could be a way to reduce or eliminate Bullfrog populations. Moreover, limiting the spread or intentional introduction of such ‘‘facilitator’’ species may help limit the spread or abundance of Bullfrogs. This hypothesis is supported by field surveys in Oregon, showing that Bullfrogs are less likely to occur and appear to be less abundant at sites lacking introduced centrarchids compared to sites with centrarchids present (Adams *et al.* 2003).

This research also suggests a hypothesis that indigenous macroinvertebrates can resist Bullfrog invasion or help restrict Bullfrog populations to low enough densities that indigenous species can persist. Research is needed to understand the factors that regulate the abundance of predaceous macroinvertebrates and their effectiveness as Bullfrog predators. Such research might indicate features of wetlands that could be manipulated to manage the Bullfrog problem.

LIVING WITH INVASIVE SPECIES

Invasive species research and management have typically centered on prediction, prevention, and eradication (Mack *et al.* 2000, Simberloff *et al.* 2005). In the early stages of invasion, aggressive actions to eradicate the invader are warranted and, in some cases, intensive efforts to directly control invaders may be preferred even after broad establishment. However, many aggressive invaders like the Bullfrog, once established, are difficult or impossible to directly control or eradicate (e.g. Mack *et al.* 2000). Even if viable approaches for eradication exist, substantial resources are seldom available for any but the most economically damaging species. Moreover, intensive efforts to eradicate can sometimes have negative side effects (Zavaleta *et al.* 2001, Maret *et al.* 2006). These factors can leave few options for managing the problem.

The difficulty in eradicating Bullfrogs, particularly over large areas, is a common situation in invasive species management and may lead to a sense of futility. However, many of the non-eradication options discussed above have not been adequately explored and have the potential to promote the persistence of some indigenous species despite the invasion of Bullfrogs. In particular, while

Bullfrogs are a problem for a variety of indigenous species and there is also evidence that some otherwise vulnerable natives can sometimes coexist with Bullfrogs (Kiesecker and Blaustein 1997, Adams 1999, Govindarajulu 2004, Pearl *et al.* 2004). Coexistence suggests that other factors such as habitat conditions can mitigate the negative effects of Bullfrogs. Management options that focus on indigenous species persistence have potentially broad application but have received little research relative to more direct eradication and control measures.

We suggest that indigenous species persistence might be a primary goal of managers that have broadly established Bullfrog populations with little hope of eradication. However, managers must also consider the characteristics of the indigenous species when setting goals. It seems likely that some indigenous species simply may not be able to coexist with Bullfrogs while others, though vulnerable to negative effects, might benefit from efforts to promote their persistence despite the presence of Bullfrogs. Indigenous species are more likely to coexist with invaders such as Bullfrogs if natural history and microhabitat preferences of the former limit spatial and temporal overlap with the invader. This is likely to be particularly important during life history stages that are demographically influential.

Consider two pond-breeding ranid frogs that historically co-occurred in lowlands of north-western North America: Northern Red-Legged Frogs and Oregon Spotted Frogs (*Rana pretiosa* Baird and Girard). There is some evidence of decline for both species but Oregon Spotted Frogs have experienced the greatest losses. Bullfrogs have been implicated in population losses of both species, and both use the same general habitats as Bullfrogs in the region. Several factors indicate that Northern Red-Legged Frogs might be more likely than Oregon Spotted Frogs to coexist with Bullfrogs (Pearl *et al.* 2004). First, experimental trials in mesocosms showed that, given a choice between land or water, Oregon Spotted Frogs and Bullfrogs both chose water more often than Northern Red-Legged Frogs. This difference in microhabitat use could reduce contact between Bullfrogs and Northern Red-Legged Frogs. Second, this same study found that, when all three species are placed together in a mesocosm with both land and water available, juvenile Oregon Spotted Frogs do not survive as well as juvenile Northern Red-Legged Frogs. This supports the notion that differences in microhabitat use help protect Northern Red-Legged Frogs from Bullfrog predation. Third, larval Northern Red-Legged Frogs are able to modify risky behaviors in the presence of cues of invasive predators including Bullfrogs (Kiesecker and Blaustein 1997, Pearl *et al.* 2003). Fourth, juveniles of the Northern Red-Legged Frog tend not to linger around breeding ponds (Nussbaum *et al.* 1983, C. Pearl 2000, personal observation) and the adults spend much of their lives away from their breeding sites (Licht 1969, 1986). In contrast, post-metamorphic Oregon Spotted Frogs, like Bullfrogs, remain closely tied to aquatic habitats throughout their lives (Licht 1969, 1986, Pearl *et al.* 2004). Finally, field surveys at sites where both natives were known to occur found Northern

Red-Legged Frogs persisting after Bullfrog invasion more frequently than Oregon Spotted Frogs (Pearl *et al.* 2004).

Another example exists within the native range of the Bullfrog in Ontario, Canada, where Green Frogs (*Rana clamitans* Latreille), which share aquatic habitat with Bullfrogs, responded positively to local Bullfrog extinction (Hecnar and M'Closkey 1997). The relative abundance of Northern Leopard Frogs (*Rana pipiens* Schreber), which use aquatic habitats favored by Bullfrogs less than Green Frogs, decreased after the same Bullfrog extinction (Hecnar and M'Closkey 1997). In general, highly aquatic species such as the Oregon Spotted Frog may not be good candidates for coexistence with Bullfrogs whereas a species like the Northern Red-Legged Frog, despite having breeding sites in common with Bullfrogs, has greater potential to coexist with Bullfrogs. A detailed understanding of behavioral and life history characteristics of indigenous species may provide clues to their vulnerability to invasive species. Such insights can inform management prescriptions, including when to consider aggressive control efforts and when to focus on the persistence of natives.

CONCLUSIONS

There are no easy solutions to the Bullfrog problem but there is hope for progress. Given sufficient resources, eradication is an option for small isolated ponds and, if possible, should be emphasized when endangered indigenous species with vulnerable natural history characteristics are involved. When this fails, there is evidence that some indigenous amphibians can coexist with Bullfrogs in some habitats despite negative effects of Bullfrogs. This gives us reason to believe that managing habitat and community characteristics has potential to promote coexistence. Our primary thesis is that further research could lead to management options that promote the persistence of indigenous species despite the ongoing presence of Bullfrogs and that such options have been neglected. This conclusion is somewhat dependent on the assumption that observed coexistence between some indigenous species and Bullfrogs is not simply a transitory condition but rather is a function of species and site characteristics.

Several lines of inquiry need increased attention to develop management options for Bullfrogs in regions where they are well established or cannot otherwise be directly eradicated. These include:

1. Temporal dimensions of coexistence: Are cases of observed coexistence transitory or related, at least in part, to local conditions? This is a critical question whenever comparative studies based on patterns of coexistence are being used to suggest that certain habitat features might promote coexistence.
2. Habitat mediation: How do physical attributes of water bodies and upland habitats affect Bullfrog abundance and interactions with indigenous species?

Are there attributes that promote coexistence with some species? If so, are there ways to manage these attributes to benefit indigenous species?

3. Invasion resistance: What features of indigenous communities can help resist Bullfrogs? Options that prevent invasion are obviously desirable but there may also be options that help constrain Bullfrogs to low numbers. Despite evidence that some odonates are voracious predators of Bullfrog tadpoles, there is little information addressing interspecific differences in predation rates or habitat features that promote various odonate species. How can beneficial species be encouraged?
4. Mutualism: Are some NIS facilitating further invasion? Can knowledge of positive interactions among NIS be used to manage invasives? This is a new topic in invasive species research but a link has already been identified between non-indigenous fish and Bullfrogs (Adams *et al.* 2003). There is potential for other mutualistic interactions to be important.

In conclusion, we emphasize that while the Bullfrog invasion problem may seem discouraging, there are management options both existing and in need of further research that give reason to hope for future progress.

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