

INFORMATION USE IN ANURANS: HOW CONSPECIFICS AND PREDATORS
INFLUENCE REPRODUCTIVE DECISIONS

BY

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DISSERTATION

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ABSTRACT

The choice of breeding habitat is integral to offspring survival and reproductive success, and can ultimately influence species distributions and population dynamics. Many factors are likely involved in location and evaluation of habitat, including biotic factors such as the presence of conspecifics and predators. Increasingly, organisms in a variety of taxa have been found to incorporate information on conspecifics and predators in their habitat selection decisions, but the degree to which this occurs in anuran amphibians is still not well-known. My research sought to first synthesize our current understanding of how conspecifics and predators influence reproductive decisions in anurans by reviewing the literature on this topic. Through experimental studies, I then examined how conspecific cues in the form of chorus sounds influenced breeding habitat selection in seven species of anurans (wood frog, *Lithobates sylvaticus*; Cope's gray treefrog, *Hyla chrysoscelis*; American toad, *Anaxyrus americanus*; green frog, *Lithobates clamitans*; spring peeper, *Pseudacris crucifer*; Mexican spadefoot, *Spea multiplicata*; and Arizona treefrog, *Hyla wrightorum*). I then further examined how the presence of conflicting cues, in this case conspecific cues and predators, influenced breeding habitat selection in a single anuran species (western chorus frog, *Pseudacris triseriata*).

A review of over 40 studies examining the influence of conspecifics, heterospecifics and/or predators on temperate and tropic anuran reproductive decisions found that in the majority of cases (75%), individuals avoid depositing offspring in sites with predators and conspecifics or heterospecifics. From my own experiments in Illinois, Indiana, and Arizona, I found that some species were attracted to breeding ponds with conspecific chorus sounds (Cope's gray treefrog and Mexican spadefoot), while others showed weak or no response to conspecifics (wood frog, American toad, green frog, spring peeper, Arizona treefrog). Response was not predictably

correlated with particular life history traits, but the tendency to breed in more seasonal or temporary ponds was a characteristic of the two species that responded more strongly to conspecific cues. Regarding the influence of predator cues on breeding pond selection of western chorus frogs, chorus frogs exhibited predator avoidance at the Illinois field site but did not vary their behavior at the Indiana field site when presented with both predators and conspecific egg-mass cues. My results provide support for the idea that some species of anurans can and do use conspecific social information in locating and selecting breeding habitat, but that social information use may vary by breeding ecology, landscape matrix, and environmental characteristics.

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CHAPTER 1: GENERAL INTRODUCTION

Social information, or information derived from observations of others in the environment, is increasingly recognized as a major force shaping animal decisions and behavior (Danchin et al. 2004, Blanchet et al. 2010). Indeed, one of the key processes in an organism's life is the selection of breeding habitat, which may ultimately be influenced by social information from conspecifics or heterospecifics (Doligez et al. 2002). Many studies have demonstrated the intersection of social information and breeding habitat selection for a variety of taxa, including birds, lizards, and insects (Stamps 1987, Schuck-Paim and Alonso 2001, Ward and Schlossberg 2004). However, the importance of social information on breeding habitat selection has been relatively overlooked for anuran amphibians. Moreover, little is known about how social information from conspecifics might interplay with other factors involved in the habitat selection process. Here I investigated the influence of social information on breeding habitat selection in anurans. Overall, my aim was to determine whether conspecific cues and predators are used by anurans to make habitat selection decisions and how cue use might vary based on species, life history, and environmental characteristics.

Research on anuran behavior and reproductive decisions dates back several decades (e.g. Resetarits and Wilbur 1989, Crump 1991). In Chapter 2, I review our current understanding of how conspecifics and predators influence anuran reproductive behavior based on published experimental and observational studies. Frequently, these experimental studies show that anuran breeding habitat selection follows the classic ideal free distribution proposed by Fretwell and Lucas (1970), where adults prefer unoccupied habitat rather than occupied habitat, given equivalent conditions in both (Resetarits & Wilbur 1989, Murphy 2003, Glos et al. 2008). However, research on other organisms has revealed that at low to moderate densities, individuals

might actually be attracted to and garner fitness benefits from conspecifics (Allee 1951, Stamps 1987, Stamps 2001). Often, the exact mechanisms for this attraction are unknown, but conspecific presence may signal habitat location or resource quality (Valone and Templeton 2002, Fletcher 2006). Thus, conspecific cues may allow individuals to quickly locate and evaluate habitat rather than directly sampling a variety of potential sites themselves (Valone 2007). Use of social information in this way is more likely to occur when direct sampling is costly (e.g. high locomotor/movement costs or predation risk) or when individuals are unfamiliar with the environment (Szymkowiak 2013).

For anuran amphibians, it has long been hypothesized that individuals use conspecific chorus sounds to facilitate location of breeding habitats (often referred to as the chorus attraction hypothesis), but surprisingly little field evidence for this idea exists (Gerhardt and Huber 2002, Gerhardt and Bee 2007). To date, research on anuran communication has mainly focused on how calls function in mate attraction and male-male competition (Gerhardt 1994). Indeed, calls convey information on species identity, location, size, and attractiveness of individual caller (Wells and Schwartz 2006). While perhaps not the main function of calls, calls may also inadvertently inform individuals of location of breeding habitat and aggregations (Swanson et al. 2007). Several laboratory-based phonotaxis experiments have found that certain species (e.g. barking treefrogs, *Hyla gratiosa*; wood frogs, *Lithobates sylvaticus*; American toads, *Anaxyrus americanus*; Cope's gray treefrogs, *Hyla chrysoscelis*) will orient towards chorus sounds emanating from a speaker (Gerhardt and Klump 1988, Bee 2007, Swanson et al. 2007). These studies often suggest that responsiveness to chorus sounds is likely influenced by species' breeding ecology, with temporal or spatial patterns in reproduction contributing to conspecific call use. For example, species breeding explosively or in seasonal ponds might be more likely to

use cues than species breeding over an extended period or in permanent ponds (Bee 2007). These temporal and spatial patterns may also interact with each other to influence strength of response.

In Chapter 3, I examine whether conspecific chorus sounds influences the location of new breeding habitat by two anuran species with contrasting breeding patterns. To do this, I broadcast playbacks of chorus sounds at a series of artificial breeding ponds for Cope's gray treefrogs and American toads in Indiana and monitor subsequent colonization. I predict that while both treefrogs and toads should colonize playback ponds faster and more often than silent control ponds, toads should have a weaker response to playbacks while they are an explosive breeder, they breed only in a permanent wetland on site.

In Chapter 4, I expand on the question of how differing breeding characteristics influence strength of response by testing multiple species of anuran to chorus sound playbacks broadcast at artificial ponds. Additionally, I perform this work across three distinct localities (and habitats) to better understand how larger environmental or landscape characteristics contribute to responsiveness. I predict that species that breed in more permanent ponds will be less likely to respond to calls compared to species that breed in more temporary or seasonal ponds. I also predict that response will be stronger for those species that breed in arid environments where rainfall is unpredictable and breeding ponds are scarce. Additionally, I expect to see a relationship between duration of breeding season and strength of response.

While conspecific calls may facilitate orientation to breeding ponds, other cues may influence habitat selection upon arrival. Both conspecifics and predators appear to play an important role in determining pond choice. Artificial pool studies have found that when given a choice between ponds with and without predators, adults preferentially oviposit in ponds without predators (Binckley & Resetarits 2003, Brown et al. 2008, Vonesh et al. 2009, Kraus et al. 2011).

Similarly, ovipositing adults tend to avoid artificial pools with larval conspecifics if equivalent, unoccupied habitat is nearby (Resetarits & Wilbur 1989, Murphy 2003, Glos et al. 2008). These findings are not surprising given the lethal effects of predators (Wilbur 1997, Relyea 2007) and non-lethal, yet still damaging, effects of competition (Wilbur and Collins 1973, Wilbur 1980, Van Allen et al. 2010). However, these studies may not necessarily be reflective of conditions experienced by breeding adults in the field where multiple biotic cues may be present in a single pond, ponds may be separated by hundreds of meters rather than tens of meters (as is often the case in artificial pool studies), and where ponds have a previous history of colonization. In these more variable conditions, predator avoidance might be lessened. Further, conspecific eggs could be used to signal habitat quality to ovipositing anurans, and thus might result in attraction rather than avoidance (Rudolf and Rödel 2005, Lin et al. 2008). Additionally, in ponds where both conspecific eggs and predators are present, eggs might negate predator effects if they are used (albeit, misleadingly) as a cue of safety or quality. In Chapter 5, I examine how the presence of fish predators (*Gambusia affinis*) in half of my artificial ponds influences subsequent colonization by western chorus frogs (*Pseudacris triseriata*). In a separate experiment at a different location, I examine how both the presence of predators and conspecific egg masses influences colonization by the same species. Because of the severe consequences of breeding in ponds with predators, I predict that in both experiments, chorus frogs should exhibit avoidance of ponds containing fish predators regardless of other factors such as prior history of site use and presence of conspecifics.

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CHAPTER 2: REPRODUCTIVE DECISIONS IN ANURANS: A REVIEW OF HOW PREDATION AND COMPETITION AFFECTS THE DEPOSITION OF EGGS AND TADPOLES¹

ABSTRACT

Selection of breeding habitat has broad-scale implications for species distributions and community structure and smaller-scale ramifications for offspring survival and parental fitness. In anurans, offspring deposition is a decision-making process that involves the assessment of multiple factors at a breeding site including the presence of predators and competitors. Evolutionary theory predicts that adult anurans should seek to minimize the risk of predation to offspring, reduce the pressure of competition, and maximize survival of offspring. Many experimental studies have examined the ability of anurans to assess deposition sites for predation and competition and choose accordingly, but our understanding of the various ecological factors involved in site choice and the broader consequences of choice is still limited. Here we review and synthesize the literature on the influence of predators and competitors on anuran deposition behavior. We highlight current gaps in our understanding of this topic and outline future avenues of research.

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INTRODUCTION

For mobile organisms, habitat selection plays a crucial role in structuring populations and shaping communities dynamics (Morris 2003). Breeding habitat selection, in particular, may influence population recruitment, parental fitness, and offspring survival (Resetarits 1996). For those organisms that attend to their offspring (e.g. most birds and mammals; Klopfer 1981), the effects of poor habitat selection decisions can potentially be minimized through parental care. But for those organisms with precocial or unattended young, habitat selection may be the only way in which parents can provide an advantage to offspring (Refsnider and Janzen 2010). Because most species of anuran amphibians (i.e. frogs and toads) deposit their eggs or tadpoles in wetlands and do not return, the decision of where to breed can subsequently have profound impacts on species distribution and viability (Woodward 1983, Wellborn et al. 1996). Investigation of the factors that influence these seemingly small-scale reproductive decisions has revealed fascinating insights into anuran ecology and behavior. Ultimately, a thorough understanding of these decisions will help inform conservation strategies and management actions for this declining group of species (Resetarits and Silberbush 2016).

Classic habitat selection theory suggests that organisms choose habitat that maximizes their individual fitness (Fretwell and Lucas 1970). Because offspring survival is a key component of fitness (Crump 1991), theory predicts that individuals should select habitat for their offspring that minimizes any risk or threats to survival (Resetarits 1996). For the large majority of anurans, habitat for eggs or tadpoles requires some form of standing water (Duellman and Trueb 1986, Wells 2007) and selection of a suitable deposition site is likely to be of particular importance because most anuran species provide no parental care and larvae are relatively confined until metamorphosis (Crump 1974, Binckley and Resetarits 2003). Both

abiotic and biotic threats may threaten offspring survival, with primary biotic threats including the presence of competitors and predators contained within these water bodies (Heyer et al. 1975, Morin 1983, Wilbur 1987). A single predator may eliminate an entire clutch of eggs, resulting in annual reproductive failure for an individual (Grözinger et al. 2011). Predators can not only cause direct mortality of young, but induce morphological, behavioral, and immunological changes in larvae that may affect survival in post-metamorphic stages (Wilbur 1997, Relyea 2007, Groner et al. 2013). Competitors may indirectly affect larval survival and time to and size at metamorphosis (Wilbur 1987), and cause detrimental carry-over effects in later life stages (Wilbur 1997, Van Allen 2010, Groner et al. 2013). As such, anurans should be selective in deposition sites because failing to do so may lead to extreme fitness consequences.

The ability to detect potential threats to offspring—such as predators—and discriminate among sites based on these threats should be more likely to evolve under particular conditions. Blaustein (1999) posited that amphibians are more likely to respond to predators when offspring are highly vulnerable to the predator (i.e. predator causes high mortality), when the predator occurs patchily throughout the landscape and is relatively common and predictable (e.g. predator does not enter and leave sites at random), and when adults have a number of available breeding sites to choose from. These conditions are often met for anurans that place their offspring in pools, particularly temporary or ephemeral pools (Blaustein 1999).

Considerable research has focused on elucidating the decisions anurans make when faced with the choice of where to deposit their eggs or tadpoles, as well as the mechanisms by which anurans gather information regarding quality or riskiness of a site. Experimental studies dating back several decades first examined the ability of anurans to detect and respond to predation or competition risk through choice experiments (Resetarits and Wilbur 1989, Crump 1991). In these

manipulations, individuals had the option of pools with or without predators or competitors. Given that individuals are able to perceive differences in risk level, they should choose to deposit eggs in pools without these biotic risk factors. The outcome is often as predicted, with individuals avoiding deposition in risky pools (Downie et al. 2001, Brown et al. 2008, Touchon and Worley 2015). However, anuran perception of predation risk is rarely straightforward and site choice has been shown to vary depending on the density, size (Spieler and Linsenmair 1997), and stage of predators or competitors (Iwai et al. 2007), and may even vary temporally and seasonally (Poelman and Dicke 2007). Experiments have accordingly become more complex, with investigators simultaneously manipulating multiple biotic and/or abiotic factors to examine ecologically-relevant trade-offs in oviposition site choice (Binckley and Reser 2008, Touchon and Worley 2015). Predicted outcomes in these experiments are less clear, but such scenarios are more likely to reflect the decisions individuals encounter in natural settings and thus provide valuable insights into anuran breeding site selection behavior.

The literature on anuran offspring deposition site choice in relation to biotic factors is sizeable and continues to grow. Accordingly, a synthesis of this information is needed to clarify our understanding of deposition site selection in anurans and highlight opportunities for further research. In this study, we review the literature on the role of predation and competition in anuran offspring deposition site choice (here offspring deposition includes nest, egg, and tadpole placement). While we recognize that other factors play a critical role in deposition decisions (e.g. hydroperiod, water temperature, canopy cover), investigating all such factors was beyond the scope of this review. We have included both experimental and correlational field studies, but we have focused more attention on experimental studies that have examined adult choice while

controlling for confounding detection effects (e.g. egg or tadpole predation) that could potentially bias results.

In the first section of this review, we examine how predation risk by non-anurans and predatory anuran larvae affects offspring deposition site choice. In the second section, we examine how the presence of conspecific or heterospecific anurans affects site choice. In the third section, we provide a general synthesis of our understanding of anuran site selection and discuss the implications for anuran ecology, conservation, and future research.

FACTORS AFFECTING OFFSPRING DEPOSITION SITE CHOICE

Predation risk

The presence of predators can present one of the most significant challenges to successful reproduction by anurans (Morin 1983, Wilbur 1987, Werner and McPeck 1994). Depositing offspring at a site with predators can result in complete reproductive failure, which may be especially problematic for short-lived anurans with few opportunities to breed. While some species have evolved adaptations to minimize risk of predation, such as breeding earlier in the year, breeding synchronously, or even producing chemical and mechanical defenses of eggs and tadpoles, other species have little or no defense against predators (Wilbur 1997, Wells 2007). For these species, habitat selection is likely an important means of reducing risk of predation to offspring (Binckley and Resetarits 2002, Rieger et al. 2004). The favored approach for experimentally examining how presence of predators affects deposition site choice has been to provide a choice of breeding sites (with and without predators or predator cues) to depositing individuals. In these studies, predators include both non-anurans (e.g. fish and arthropods) and predatory anuran larvae. In the following sections, we review the results from these experimental

studies. We also highlight results from a review of correlational field studies associating the presence of fish predators to the presence or abundance of anurans. Because there has been a large number of correlational studies, we recognize that some studies may have been overlooked and we direct readers to previously published review papers by Kats and Ferrer (2003) and Bucciarelli et al. (2014) detailing the effects of alien predators on amphibian populations.

Predation risk by non-anurans

We reviewed 17 experimental studies examining the effects of predation risk by non-anurans on anuran deposition site selection. These studies used 13 anuran species from 6 different families (Table 2.1). Of the 13 species, 7 are found in the tropics while the remaining 6 are found in temperate regions. The majority of studies used or included fish as their predator of interest ($n = 13$ studies), although insects ($n = 5$), fairy shrimp ($n = 1$), salamander larvae ($n = 1$) and adult newts ($n = 1$) were also used. In addition, the majority of studies ($n = 14$) were conducted using artificial pools placed in the field, while two studies added predators to natural or seminatural pools and one study examined deposition behavior in the laboratory. Several studies examined multiple anurans ($n = 3$) and several ($n = 3$) simultaneously manipulated predation risk and another risk factor (i.e. competition risk and desiccation risk), ultimately resulting in 32 unique tests of predator avoidance. Those experiments that did not provide a predator-free option for deposition site were not included in the total count of unique tests of avoidance. In most cases, the response variables included the number of eggs or egg masses laid ($n = 22$ tests), although the number of tadpoles deposited ($n = 7$), and number of nests built ($n = 3$) were also examined. All of the studies described how they ensured that their results were not skewed by any undetected egg or tadpole depredation.

In the reviewed studies, anurans chose to oviposit in predator-free pools in 78% (25 of 32) of predator tests (Fig. 2.1). In the other 22% of cases in which anurans deposited offspring in pools containing predators, the authors suggested or identified ecologically-relevant explanations. For instance, Cope's gray treefrogs, *Hyla chrysoscelis*, did not show avoidance of adult newts, *Notophthalmus viridescens dorsalis*, perhaps because newts are relatively common throughout the landscape and are mobile predators, making it difficult for adults to evolve avoidance behaviors (Reser and Wilbur 1989). Females of a neotropical frog species, *Edalorhina perezi*, showed no avoidance behavior to dragonfly naiad predators, *Aeshna odonate*, late in the breeding season despite showing avoidance earlier in the breeding season, perhaps because adults are willing to accept less desirable sites as breeding pressure increases and time becomes limited (Murphy 2003a). In the common frog, *Rana temporaria*, females continued to lay eggs in pools to which sticklebacks, *Gasterosteus aculeatus*, had been added (Laurila and Aho 1997). Unlike the majority of studies reviewed here, this study added fish to pools with a prior history of colonization by anurans (rather than newly established, uncolonized pools), leading the authors to speculate that fidelity to a particular breeding pool may have resulted in maladaptive behavior by preventing females from behaving as flexibly as seen in other studies using newly created ponds. Alternatively, fish colonization of ponds may be such a rare event that common frogs have not evolved avoidance behavior to fish (Laurila and Aho 1997). In a final example of non-avoidance behavior, an explosive ephemeral pond breeding toad, *Melanophryniscus rubriventris*, continued to oviposit in pools to which water bugs, *Belostoma* spp., had been added (Laufer et al. 2015). In this system, other selective abiotic pressures, such as desiccation risk, may have been more important in determining oviposition site than predator avoidance (Laufer et al. 2015).

Surprisingly, some anurans appear capable of perceiving danger from a particular predator even when they have no prior experience with that species. When given a choice between pools containing an unfamiliar predator (either fairy shrimp, *Macobrachium* spp., or piscivorous fish, *Rivulus hartii*, depending on origin of test frogs) and control pools with no predator, males of the Trinidadian stream frog, *Mannophryne trinitatus*, resoundingly deposited their tadpoles in predator-free pools (Downie et al. 2001). When given a choice between pools containing a familiar predator and an unfamiliar predator, many males avoided depositing in either pool, and instead eventually deposited tadpoles in leaf litter (Downie et al. 2001). Females of the neotropic pantless treefrog, *Dendropsophus ebraccatus*, were similarly able to discern fish predators (*Astyanax ruberrimus*) in artificial tubs despite no prior experience with the particular fish predator, suggesting that avoidance of predator cues may be innate (Touchon and Worley 2015). However, the ability to recognize unfamiliar species as predators likely varies among anurans, and may depend on evolutionary history with the predator, taxonomic or behavioral similarity of unfamiliar to familiar predators, and the specificity or generality of cues used to recognize predators (Carthey and Banks 2014).

Predator avoidance may not always be entirely straightforward if other biotic or abiotic risk factors are manipulated simultaneously. While few studies have directly examined a predation-competition tradeoff in oviposition site selection, Murphy (2003a) found that Perez's snouted frog (*Edalorhina perezii*) females preferred the indirect risks of offspring competition to the direct risk of offspring mortality by dragonfly naiads. Anurans may also prefer an unknown amount of abiotic risk to the direct risk of predation, as Touchon and Worley (2015) observed with pantless treefrog mating pairs. When fish predators were not present, treefrogs laid $\geq 80\%$ of their eggs aquatically. When predators were present, mating pairs laid $\leq 20\%$ of their eggs

aquatically, instead choosing desiccation risk associated with arboreal oviposition rather than aquatic predation risk. While mortality due to predation is almost certain, mortality due to desiccation is unpredictable. Whether anurans may be willing to accept more risk if there is a corresponding increase in “reward” has been little examined, although Binckley and Resetarits (2008) found that increasing resource (i.e. food) levels in ponds with high fish densities had no effect on squirrel treefrog, *Hyla squirella*, or Cope’s gray treefrog oviposition behavior. Thus, their original hypothesis that treefrog females would accept greater levels of risk if resource levels were elevated was not supported. Interestingly, several studies have found that avoidance of fish pools may be compromised on nights with elevated breeding activity, as fish free pools become saturated with conspecific eggs and adults seek out alternative breeding sites that may contain fish but few conspecifics (Rieger et al. 2004, Binckley and Resetarits 2008, Kraus and Vonesh 2010). This behavior is consistent with the predictions of the ideal free distribution model of habitat selection, where the highest quality habitats should be chosen first and as those habitats become saturated, lower quality habitats become occupied (Fretwell and Lucas 1970).

A review of 37 correlational studies of 32 anuran species from four families associating fish predator presence with anuran presence or abundance yields much more mixed patterns than experimental studies (Appendix A, B). Thirty-four percent of anuran species were negatively associated with the presence of fish, 9% showed positive associations, 16% showed no association, and 41% displayed mixed associations where response varied by study. Species in the family *Hylidae* consistently showed negative associations with fish, while *Bufo* species often showed positive or neutral associations with fish. Responses in the family *Ranidae* appear much more species-specific, where bullfrogs, *Lithobates catesbeianus*, and green frogs, *Lithobates clamitans*, often showed positive or neutral associations, while mountain yellow

legged frogs, *Rana muscosa*, consistently showed negative associations. Most of the studies surveyed multiple life stages of anurans (egg, tadpole, juvenile and adult) at breeding sites, with and without the predator of interest, and combined life stages in analysis (i.e. for a site to be considered occupied, it need only contain at least one of the life stages). Combining life stages renders it impossible to discern if decreased occupancy or abundance in ponds containing predators is a result of direct avoidance by adults of predator ponds, or rather a byproduct of predation on eggs and larvae. Regardless, from these studies it is apparent that not all species use habitat selection as the first line of defense in minimizing risk of predation; some species have evolved specific anti-predator mechanisms to successfully coexist with predators (Appendix A, B).

Predation risk by anurans

We reviewed 16 studies examining deposition site selection in the presence of predatory anurans for 11 focal species from six families (Table 2.2). The majority of these studies manipulated initial conditions at a breeding site by adding predatory tadpoles ($n = 10$ studies) to a pool, although in some cases chemical cues of tadpoles ($n = 3$) or eggs ($n = 4$) of predatory species were added. In several cases ($n = 5$) natural colonization of pools was allowed. Choice was then compared between pools with predators and pools containing “blank” or untreated water. Two studies investigated seasonal variation in deposition behavior, two studies considered how stage or size of predatory anuran affected behavior, and one study manipulated predation risk simultaneously with another risk factor. Collectively, there were 36 tests of predator avoidance. Response variables measured in these studies included the number of eggs or egg masses laid ($n = 20$ tests) and the number of tadpole depositions ($n = 16$).

In the majority of tests (72%, 26 of 36), adults avoided depositing eggs or tadpoles in pools with cues from anuran predators (Fig. 2.1). However, behavior sometimes varied depending on stage or density of predators. Japanese brown frog females, *Rana japonica*, for example, avoided ovipositing in artificial pools if they contained a conspecific resident egg mass older than Gosner's stage 16, but preferred pools if the egg mass was younger than stage 16 (Iwai et al. 2007). This behavior suggests that brown frogs can perceive differences in the stage of development of conspecific egg masses and make decisions accordingly (Iwai et al. 2007), which should be adaptive if ovipositing in pools with older eggs makes new eggs vulnerable to intraspecific predation. Remarkably, some anurans can detect subtle differences in amount and size of predatory larvae using only olfactory or chemical cues. Females of the crowned bullfrog, *Hoplobatrachus occipitalis*, deposited fewer eggs in rock pools with opaque containers of high tadpole density and large tadpole size compared to rock pools with containers of low tadpole density and small tadpole size (Spieler and Linsenmair 1997). Curiously, male dyeing poison frogs, *Dendrobates tinctorius*, exhibited the opposite behavior, with males more likely to deposit tadpoles in a pool with a larger conspecific than in an unoccupied pool, but exhibited no preference in occupied or unoccupied pools if the resident tadpole was similar in size to the male's own tadpole (Rojas 2014). The reason behind this behavior is unclear, although it has been suggested that the large conspecific may indicate suitable breeding habitat. However, the costs of intraspecific predation would seem to outweigh any suspected benefits, particularly given that, in this experiment, suitable sites were not a limiting resource (Rojas 2014).

Adults also appear capable of distinguishing between egg predators and tadpole predators, as the same cues are not consistently avoided for egg and tadpole deposition. Splash-back poison frogs, *Ranitomeya variabilis*, for example, oviposit in phytotelmata (small

impounded pools of water in terrestrial plants) and then transport tadpoles to different phytotelmata after hatching (Schulte et al. 2011). Adult poison frogs avoided depositing eggs in pools with tadpole chemical cues of a bufonid toad, *Rhinella poeppigii*, but did not avoid the same cues when depositing tadpoles (Schulte et al. 2011). The authors suggested that this difference may be because toad tadpoles will consume eggs, but will not consume live tadpoles. Splash-back poison frogs exhibit a similar response to cues of other poison frog species that only consume eggs (*Ameerega trivittata*, *Hyloxalus nexipus*; Schulte and Lötters 2014). In some instances, anurans preferentially choose to deposit their tadpoles in pools already containing eggs or tadpoles as an act of reproductive parasitism (Summers 1999). Depositing tadpoles in a pool containing eggs or smaller tadpoles may provide the larger tadpole with a food source. Such behavior has been observed in highly cannibalistic splash-back poison frogs, where males preferentially deposited their tadpoles in pools with unrelated eggs (Brown et al. 2009). Poison frogs also preferentially deposited their tadpoles in pools treated with chemical cues of non-predatory treefrog larvae (*Osteocephalus mimeticus*) rather than clean-water pools, potentially because treefrog larvae may be viewed as a food source for their tadpoles (Schulte and Lötters 2014).

Adults may also parasitize their own reproductive efforts if it is advantageous to do so. In the rainy season in Peru (studied from late March to early April), splash-back poison frog males deposited significantly more tadpoles in pools within their own territories that did not contain conspecific tadpole chemical cues, while the opposite was true in the dry season (studied from early April to early June; Schulte and Lötters 2013). Similarly, as the amount of rainfall declined throughout the breeding season (from April through July), female reticulated poison frogs (*Ranitomeya ventrimaculatus*) in French Guiana were more likely to deposit a clutch in

phytotelmata already containing a descendant tadpole rather than empty phytotelmata (Poelman and Dicke 2007). The authors of these studies interpreted the seasonal differences in deposition site choice as a strategy to increase the survival chances of existing related tadpoles that may be in jeopardy as breeding pools slowly dried out. By depositing new offspring in pools, parents provide existing offspring with a food source, thus decreasing time to metamorphosis or increasing metamorph size (Poelman and Dicke 2007).

Competition: non-predatory conspecifics and heterospecifics

One of the most powerful cues available to breeding anurans may be the presence of conspecific or heteropsecific egg masses, tadpoles, or adults at or near a breeding site. However, these cues may be viewed as either positive or negative depending on the situation. On one hand, classic habitat selection theory predicts that individuals should avoid areas of high density to maximize individual and offspring fitness (Fretwell and Lucas 1970). Indeed, increased intensity of larval competition for valuable limited resources such as food and space may prolong time to and decrease size at metamorphosis, and ultimately affect larval survival (Wilbur and Collins 1973, Wilbur 1980, Van Allen et al. 2010, Groner et al. 2013). Further, density effects have been shown to carry over to postmetamorphic stages and negatively affect anuran survival later in life (Relyea and Hoverman 2003).

Conversely, it has been increasingly recognized that individuals are attracted to and preferentially settle near conspecifics or heterospecifics, a phenomenon known as conspecific or heterospecific attraction (Stamps 1987, Danchin et al. 2004, Valone 2007). Indeed, the relationship between fitness and density may actually be unimodal rather than linear, where fitness increases with low to moderate densities of conspecifics and decreases at moderate to high densities (Allee 1951, Stamps 2001). For adult anurans, depositing offspring in a pond with

conspecifics or heterospecifics could confer certain benefits that may increase rather than decrease fitness. For example, the presence of already deposited eggs or tadpoles may act as an indicator of habitat quality, allowing individuals to quickly discern whether a site is suitable for their own offspring (Rudolf and Rödel 2002). Thus, rather than sampling multiple breeding sites and incurring the costs associated with such sampling (increased energy expenditure, increased chance of predation and desiccation, less time allocated to other activities), using the presence of conspecifics may significantly reduce those costs (Ahlering et al. 2010). Anurans may also preferentially deposit offspring in already occupied ponds to reduce risk of predation via the dilution effect, cause predator satiation, derive benefits from selfish herd effects and, for certain species, receive thermal protection of eggs from cold temperatures (Hamilton 1971, Bertram 1978, Doody et al. 2009).

Compared to predation, fewer studies have examined the effects of conspecific and heterospecific presence on deposition site selection in anurans. Here we have reviewed 13 studies on this topic, 6 of which included an experiment designed to directly test the influence of anuran presence on deposition behavior by presenting individuals with a choice between control pools and pools containing conspecific or heterospecific cues (Table 2.3). The remaining studies were primarily observational in that they allowed for natural colonization of pools and correlated occupancy or abundance of eggs, larvae, or post-metamorphic individuals with the presence or abundance of conspecifics or heterospecifics.

In the majority of experimental tests (75%, or 6 of 8 tests), anurans avoided ovipositing in pools with conspecifics or heterospecifics (Fig. 2.2). In one case, Cope's gray treefrogs did not avoid ovipositing in pools with bullfrog tadpoles, likely because these species rarely encounter each other due to differences in habitat use (bullfrogs tend to occupy more permanent ponds with

fish) and so were not perceived as a competitive threat (Resetarits and Wilbur 1989). In another case, túngara frogs, *Engystomops pustulosus*, showed no preference for pools in which conspecific nests had either been removed or added, leading the authors to conclude that habitat quality may be more important in selecting habitat than conspecific presence (Marsh and Borrell 2001).

Of the observational studies reviewed, 3 studies documented co-occurrence with conspecifics or heterospecifics (aggregation occurred more often than expected by chance), 3 documented avoidance (aggregation occurred less often than expected by chance), 1 documented a seasonal effect, 1 documented a conflicting effect based on venue of experiment, and 1 found no effect. The co-occurrence or aggregation behavior observed in these studies may be a byproduct of preference for similar habitat or it may indicate a direct preference for grouping with conspecifics. Alternatively, it may also be a result of individuals using others as an indicator of habitat location and quality. These explanations need not be mutually exclusive, and unless a direct experiment is performed, or the confounding effects of habitat controlled for, it is difficult to disentangle these mechanisms. Marsh and Borrell (2001) were able to tease apart the conflicting patterns they observed with túngara frogs—where a significant preference for sites with conspecifics was observed in natural stream environments, but an avoidance of conspecifics in artificial pools—through a simple transplant experiment (discussed in previous paragraph). The results of this experiment led the authors to conclude that because all artificial pools are of equivalent habitat quality aside from the presence of conspecifics, it would benefit individuals to avoid larval competition and instead oviposit in a pond without conspecifics, whereas in natural pools, variability in habitat quality leads to conspecifics grouping in the same suitable areas (Marsh and Borrell 2001). Rudolf and Rödel (2005) also found that túngara frog females

preferentially oviposit in ponds with conspecifics, likely because the presence of conspecifics represents the overall water holding capacity of the breeding site. Indeed, correlative field studies have found that heterospecifics sometimes co-occur in the same water bodies more frequently than expected, suggesting that the negative impacts of competition may be counteracted at high-quality sites (van Buskirk 2005). In some species, there may even be a seasonal component to use of conspecifics as an indicator of breeding habitat quality. Early in the breeding season of small tropical frogs in Taiwan (*Kuraxilus eiffingeri*), adults avoided ovipositing in bamboo stumps containing conspecifics, but preferentially deposited their eggs with conspecific larvae later in the breeding season (Lin et al. 2008). In this case, larvae may be used as a reliable indicator of good quality habitat by late ovipositing adults. Clearly, there are many ways that anurans can interpret the information provided by conspecific and heterospecific cues, and that information may be context dependent.

DISCUSSION

Predation

Many studies have examined the impact of predators on offspring deposition site selection in anurans using both experimental and correlational studies. Approximately 75% (51 of 68 cases) of these experimental tests found that individuals prefer to deposit offspring in sites without predators (including both anuran and non-anuran predators), 9% found a preference for depositing in sites with predators, and 16% found no preference. Those experimental tests that did not document an avoidance response yield insight into anuran ecology and evolution that may ultimately be important for anuran conservation. Lack of predator avoidance appears both context dependent (where avoidance response depends on factors such as timing in breeding season, community composition, location or spatial structure of study, etc.) and predator

dependent (where avoidance response depends on familiarity, predictability, ubiquity, mobility of predator). For example, avoidance of predators may lessen as predator-free sites fill with other colonizers (Binckley and Resetarits 2002, Kraus and Vonesh 2010), or as the breeding season progresses (Murphy 2003a). Further, adult anurans may not have evolved avoidance behavior if predators are ubiquitous in the environment, rarely encountered (Laurila and Aho 1997), or are spatially or temporally unpredictable (Resetarits and Wilbur 1989). Predator attraction was rarely observed, but occurred most often in the presence of predatory anurans (5 of 6 cases), rather than non-anuran predators (1 case). Depositing offspring in areas already containing predatory anuran larvae largely appears to be related to intra- or inter-individual reproductive parasitism: depositing younger offspring in pools with related, older offspring may provide a food source to an adult's older offspring (Poelman and Dicke 2007, Brown et al. 2009, Schulte and Lötters 2013), while younger or earlier stage unrelated offspring may similarly act as a food source (Schulte and Lötters 2013).

We found a bias in the species used in predator-choice experiments, with species from the genus *Hyla*, *Ranitomeya*, and *Dendrobates* being among the most common subjects. Additionally, most of the species experimentally tested breed in seasonal or temporary wetlands. While it may be less likely for permanent pond breeders to evolve selective deposition behavior, testing species that breed in a wider range of hydroperiods may clarify the patterns observed here and further elucidate the evolution of deposition behavior. Indeed, we recognize that our ability to draw conclusive patterns on deposition behavior and predators is limited by the small number of species experimentally examined. Although this species bias is likely a function of logistical constraints (e.g. established study areas, ease of setting up small experimental ponds), a more

thorough understanding of anuran site selection requires research on a broader range of species and systems.

While the majority of experimental studies generally indicate a negative response to predators, the associations between predator presence (typically fish) and anuran occurrence or abundance in correlational field studies show more mixed patterns across species. Although adult choice is rarely addressed in correlational studies, these studies demonstrate the variability and context dependent nature of anuran response to predators, even within individual species. For example, Hopey and Petranka (1994) found that all wood frog (*Lithobates sylvaticus*) breeding in North Carolina, U.S. occurred in fishless ponds, concluding that wood frog adults likely assess ponds prior to breeding. Conversely, Eaton et al. (2005) found no difference in number of wood frog adults between fish and fishless ponds in Alberta, C.A. concluding that adults probably breed indiscriminately because wood frogs are highly philopatric and have little time to sample ponds before breeding. Discrepancies such as this illustrate the need for further studies on the role of adult choice in affecting patterns of observed distributions in relation to predator presence. Further, these studies illustrate that certain species rely on particular adaptations to minimize risk of predation, rather than selecting sites without predators. For example, many anuran species that inhabit more permanent water bodies have evolved unpalatable or less physically active larvae than temporary pond breeders (Wells 2007). Some species also breed synchronously, or produce large quantities of eggs to decrease overall predation risk via predator satiation (Crump 1974, Doody et al. 2009). Indeed, Crump (2015) suggests from her work on predatory anuran larvae in the tropics that adults of prey species do not choose sites lacking predatory tadpoles or adjust timing of breeding to minimize overlap, but

instead produce mass quantities of eggs and, in some cases, provide protection to the early egg stage.

For those species that do actively assess predation risk at a breeding site, our understanding of the mechanisms used to detect predators is minimal and many questions remain unanswered. While chemical cues are oft cited as a primary mode of predator detection (e.g. Binckley and Resetarits 2003, Rieger et al. 2004), little is known about the quantity of cue needed to elicit a response, proximity individuals must be in to detect a cue, how the abundance of other anurans affects the ability to detect a cue, and how detection ability may vary by species, sex, and age. Other cues may also be used to detect predator presence, such as visual or auditory, but the importance of each in the context of reproductive site choice has not been thoroughly explored. From the studies reviewed here, it appears that at least some species of anurans have a highly refined sensory ability and can detect very low levels of predator cues or identify predation risk based on age of predatory larvae (Spieler and Linsenmair 1997, Iwai et al. 2007). Pinewoods treefrog females (*Hyla femoralis*), for example, are capable of detecting and avoiding ponds containing very low densities of predatory eastern mudminnows (*Umbra pygmaea*, <0.5 g fish/100 L; Rieger et al. 2004).

The ability of anurans to recognize cues of unfamiliar predators also requires further investigation. Although two studies described earlier found that adults avoid depositing offspring in pools with unfamiliar predators, the ubiquity of this behavior is unknown. Indeed, many field studies have correlated declines in native species to invasive predator presence, but it is unclear whether adults actually detect and avoid ovipositing in breeding habitats containing invasive predators. While several studies have examined larval anuran response to invasive species (e.g. Kiesecker and Blaustein 1997, Nunes et al. 2013), few have experimentally examined adult

response, particularly in the context of egg or tadpole deposition behavior. As has been observed with larvae, the ability of adult anurans to recognize unfamiliar predators may depend on a variety of factors, such as the time since introduction, the prior presence of functionally similar predators, or the specificity or generality of cues used to detect predators (Bucciarelli et al. 2014, Carthey and Banks 2014). Comparing deposition behavior in populations that differ in predator invasion history may provide insight on the ability of anurans to evolve and respond to selective pressures. Ultimately, such research could have important conservation implications for species facing population declines as a result of invasive predators. For example, the failure of red-legged frogs, *Rana aurora*, to respond to predator cues of invasive bullfrogs has been implicated as a potential cause of recent population declines (Kiesecker and Blaustein 1997).

A better understanding of the trade-offs involved in deposition site choice is also needed. Only a few studies reviewed here examined trade-offs through manipulation of multiple factors (e.g. desiccation vs predation risk, competition vs predation risk), thus it is difficult to draw general conclusions on the type and amount of risk anurans are willing to accept in a deposition site. However, a number of studies have documented that some predation risk is preferred over high conspecific density (Rieger et al. 2004, Kraus and Vonesh 2010). Future studies investigating how choice may depend on the interaction of predation risk and other biotic or abiotic factors will advance our understanding of the complexities involved in site choice. Because not all species will respond to tradeoffs in similar ways, interpreting response in the context of life history characteristics will also be important.

Finally, additional research is needed on the role of sampling behavior and spatial dynamics in deposition decisions. Many of the experimental studies reviewed here used pools placed in close proximity to one another and have found that anurans will sample multiple

breeding pools for a suitable site (Resetarits and Wilbur 1989, Hopey and Petranka 1994). These observations raise questions regarding the number of sites anurans sample before making a decision and the spatial scale at which this sampling takes place. The search or sampling strategy used by anurans is also in question—do anurans use a comparison strategy where multiple pools are visited and, among these, the best site is selected (e.g. best-of N, pooled comparison, Bayes comparison), or do they use a sequential strategy where each pool is visited and judged according to whether it meets some minimum criteria (e.g. threshold approach; reviewed in Luttbeg 2002)? How does sampling behavior vary by individual (i.e. are some individuals more exploratory or risky in their sampling behavior than others), population, or species? In terms of spatial scale, many experimental studies typically examine deposition decisions on a single smaller scale, making it difficult to interpret how deposition behavior affects species distributions on a broader scale. Resetarits (2005), however, manipulated predator presence at both local scales and ‘regional’ scales by establishing discrete localities of pools (localities were composed of three pools in close proximity to each other containing no fish, one pool with fish, or two pools with fish) within a region. This work demonstrated that while Cope’s gray treefrogs select habitat at both scales, regional habitat selection was clearly dominant, with frogs laying far fewer eggs in any localities with fish. These observations suggest a contagion scenario where suitable predator-free pools may be deemed as unsuitable simply because they are in close proximity to predator pools, illustrating the necessity of considering placement and spatial arrangement in the creation or restoration of breeding habitat for anurans (Resetarits 2005). Further studies investigating the scale at which species make breeding site decisions will aid in our understanding of how to manage populations.

Competition: non-predatory conspecifics and heterospecifics

The literature investigating the influence of conspecific and heterospecific presence on selection of oviposition site is surprisingly sparse. Of the experimental tests, 75% demonstrated that adults avoid ovipositing in pools with conspecifics or heterospecifics, 25% documented no preference, and no studies found evidence of attraction. Avoidance behavior is typically demonstrated in studies when breeding sites are in close proximity to each other and are of equivalent habitat quality (other than the presence of potential competitors), thus allowing adults to sample multiple sites in one night. In these instances, it is probably advantageous to avoid competitors. However, when sites are located further apart, or habitat is more variable in quality, attraction to conspecifics could occur if adults are using the presence of other individuals to locate suitable habitat (Buxton et al. 2015). Indeed, in correlational field studies, aggregation is documented as often as avoidance. Aggregation may simply be a byproduct of preference for the same habitat or, as stated above, it may be a result of individuals using conspecific or heterospecific cues to preferentially settle near others (Valone 2007).

These observations raise the question of how often conspecific cues are used in site selection. This question has been frequently examined in birds and insects, where individuals have been found to select breeding habitat based on the presence of conspecifics (Ward and Schlossberg 2004, Raitanen et al. 2014). The mechanisms for this conspecific attraction may include quick identification of suitable habitat, protection from predators, and/or increased mating opportunities (Ahlering et al. 2010). In anurans, the presence of conspecifics and heterospecifics (e.g. egg masses, larvae, or adult presence) could be an important cue used in breeding site selection, yet the topic has received little attention. It is likely that response to other individuals will vary by species, ecological context, spatial context, and possibly inter-individually. However, if conspecifics or heterospecifics act as an attractant to other individuals,

regardless of mechanism, then such a response could have important conservation implications. Broadcasting conspecific chorus sounds, for example, at potential breeding sites could aid in colonization of newly created or restored wetlands (Buxton et al. 2015). Ultimately, a greater understanding of the use of social information in anuran decision-making could be important both for conservation and management of at-risk anuran populations (James et al. 2015).

CONCLUSION

From our review of over 30 studies incorporating 68 tests experimentally examining breeding site choice of adult anurans in relation to predators, it is apparent that most anurans choose to avoid depositing offspring at sites with predators. However, this decision may depend on many factors, including species life-history characteristics, timing in breeding season, and evolutionary history with predators. Our review of 13 studies examining the effect of conspecific and heterospecific cues on breeding site choice of adult anurans yields less-conclusive patterns. While adults generally avoided depositing offspring in ponds with conspecifics or heterospecifics in experimental studies, aggregation behavior was documented as frequently as avoidance behavior in correlational field studies. Deposition behavior in relation to potential competitors will likely vary based on a number of factors including abundance of competitors, location and amount of breeding habitat, and species life-history characteristics.

Much remains unknown about deposition site selection and the broader consequences of this behavior. For example, what decision rules do anurans use in selecting breeding habitat? Are decision rules innate or is there learning (e.g. experiential or social learning) involved? How do decision rules vary among individuals, populations, or species? While other taxa have been observed to employ comparative or sequential tactics in searching for and assessing habitat, such strategies have been little examined in anurans. How does scale influence selection behavior?

While deposition decisions are often viewed as acting on a small-scale, they may have larger implications for species abundances and distributions (Marsh and Borrell 2001, Resetarits and Silberbush 2016). Local variation in competitors or predators, for example, may confine individuals to or exclude individuals from certain areas, reducing the amount of habitat available (Resetarits 2005). This could, in turn, affect dispersal dynamics and population recruitment, and ultimately, species viability (Resetarits and Silberbush 2016). In a time when amphibians are experiencing precipitous and unprecedented declines, understanding how anurans make decisions regarding breeding sites and how those decisions impact reproductive success and population dynamics will help us develop more effective conservation and management strategies for at-risk populations.

TABLES AND FIGURES

Table 2. 1. Summary of experimental studies examining the effect of non-anuran predator presence on deposition site choice in anurans measured by # of eggs or egg masses deposited (E), tadpoles deposited (T), or nests built (N). Response is noted with either a – (avoidance of predator), + (attraction), or 0 (no preference).

Species	Test performed	Variable measured	Response	Reference
<i>Mannophryne trinitatis</i> (northern slope)	Fairy shrimp vs control	T	–	Downie et al. 2001 ^c
	Familiar (shrimp) vs foreign (fish) predator ^a	T	–	
	Foreign predator vs control	T	–	
<i>Mannophryne trinitatis</i> (southern slope)	Fish vs control	T	–	– (familiar) / + (foreign)
	Familiar (fish) vs foreign (shrimp) predator ^a	T		
	Foreign predator vs control	T	–	
<i>Melanophryniscus rubriventris</i>	Water bug vs control	E	0	Laufer et al. 2015
<i>Ranitomeya biolat</i>	Mosquito vs control	T	–	von May et al. 2009
<i>Ranitomeya imitator</i>	Damselfly vs control	T	–	Brown et al. 2008
<i>Ranitomeya variabilis</i>	Damselfly vs control	E, T	–, –	Brown et al. 2008
<i>Dendropsophus ebraccatus</i>	Fish vs control	E	–	Touchon & Worley 2015
	Fish vs desiccation risk	E	– (fish)	
<i>Hyla</i> spp. (<i>cinera</i> and <i>chrysoscelis</i>)	Fish vs control	E	–	Kraus et al. 2011
<i>Hyla chrysoscelis</i>	Fish vs control	E	–	Resetarits & Wilbur 1989; Resetarits 2005; Binckley & Resetarits 2003, 2008; Vonesh et al. 2009

Table 2. 1 (cont.)

	Fish vs control	E	– (reduced assembly) / + (ambient assembly) ^b	Kraus and Vonesh 2010
	Salamander larvae vs control	E	–	Resetarits & Wilbur 1989
	Newt vs control	E	0	Resetarits & Wilbur 1989
	Dragonfly naiads vs control	E	0	Resetarits & Wilbur 1989
<i>Hyla femoralis</i>	Fish vs control	E	–	Rieger et al. 2004
<i>Hyla squirella</i>	Fish vs control	E	–	Binckley & Resetarits 2002, 2008
<i>Edalorhina perezii</i>	Dragonfly naiads vs control	E, N	–, – (early season) / 0,0 (late season)	Murphy 2003a
	Dragonfly naiads vs larval conspecifics	N	– (dragonfly naiads)	
<i>Lithobates sylvaticus</i>	Fish vs control	E	–	Hopey & Petranka 1994 ^c
<i>Rana temporaria</i>	Fish vs control	E	0	Laurilo & Aho 1997 ^c

^a These tests were not included in total number of predator avoidance tests because no predator-free option was available.

^b This was a 2 × 2 factorial experiment with fish and fishless pools containing ‘ambient’ (eggs allowed to remain in pool) or ‘reduced’ (eggs removed from pool) community assembly.

^c Downie (2001) was conducted in the laboratory. Hopey and Petranka (1994) and Laurila and Aho (1997) were conducted in natural or seminatural pools. All other studies were conducted in artificial pools placed in the field.

Table 2. 2. Summary of studies examining the effect of **a)** conspecific or **b)** heterospecific predatory anuran presence on deposition site choice in anurans measured by # of eggs or egg masses deposited (E), tadpoles deposited (T), or nests built (N). Response is noted with either a – (avoidance of predator), + (attraction), or 0 (no preference).

a)

Species	Test performed	Variable measured	Response	Reference
<i>Mannophryne trinitatis</i> (northern slope)	Tadpole vs control	T	+	Downie et al. 2001 ^d
<i>Mannophryne trinitatis</i> (southern slope)	Tadpole vs control	T	–	
<i>Dendrobates tinctorius</i>	Tadpole vs control	T	0 (but + to larger tadpoles)	Rojas 2014
<i>Ranitomeya biolat</i>	Tadpole vs control	T	–	von May et al. 2009
<i>Ranitomeya variabilis</i>	Eggs vs control	T	+	Brown et al. 2009
<i>Ranitomeya variabilis</i>	Tadpole chemical cue vs control	E, T	–, –	Schulte et al. 2011
<i>Ranitomeya variabilis</i>	Tadpole chemical cue vs control	E	–	Schulte & Lötters 2013
	Tadpole chemical cue vs control	T	– (rainy season) / + (dry season)	
<i>Ranitomeya ventrimaculatus</i>	Tadpole vs control	E, T	–, –	Summers 1999 ^d
<i>Ranitomeya ventrimaculatus</i>	Tadpole vs control ^a	E	– (early season) / + (late season)	Poelman & Dicke 2007 ^d
<i>Hoplobatrachus occipitalis</i>	Tadpole vs control ^a	E	–	Spieler & Linsenmair 1997 ^d
	Tadpole high density vs low density ^b	E	– (high density) / + (low density)	
	Tadpole large vs small ^b	E	– (large) / + (small)	
	Tadpole vs herbivorous heterospecific tadpole	E	– (conspecific) / + (herbivorous)	
	Eggs vs control ^a	E	–	
<i>Isthmohyla infucata</i>	Tadpole vs control	E	–	Crump 1991

Table 2. 2a (cont.)

	Tadpole, deep water vs no tadpole, shallow water	E	0 ^c	
<i>Pleurodema borellii</i>	Tadpole small vs medium vs large ^{a,b}	N	– (large and medium) / + (small)	Halloy 2006
<i>Rana japonica</i>	Eggs vs control	E	0 (but – of masses ≥ stage 16, + to masses < stage 16)	Iwai et al. 2007

^a These tests did not manipulate initial conditions (e.g. placement of eggs or tadpoles) at breeding sites but instead allowed for natural colonization.

^b These tests were not included in total number of predator avoidance tests because no predator-free option was available.

^c Crump (1991) states that few frogs chose to oviposit in either treatment and instead oviposited in a nearby naturally-occurring pond.

^d Downie (2001) was conducted in the laboratory. Summers (1999), Poelman and Dicke (2007), and Spieler and Linsenmair (1997) were conducted in natural pools. All other studies were conducted in artificial pools placed in the field.

Table 2.2 b)

Species	Test performed	Variable measured	Response	Reference
<i>Anaxyrus americanus</i>	<i>Rana sylvatica</i> eggs vs control	E	-	Petranka et al. 1994 ^d
<i>Anaxyrus americanus</i>	<i>Rana sylvatica</i> tadpoles vs control ^a	E	-	Petranka and Holbrook 2006 ^d
<i>Melanophryniscus rubriventris</i>	<i>Pleurodema borelli</i> tadpoles vs control	E	0	Laufer et al. 2015
<i>Ranitomeya imitator</i>	<i>Ameerega trivittata</i> ^b tadpoles vs control	T	-	Brown et al. 2008
<i>Ranitomeya variabilis</i>	<i>Ameerega trivittata</i> ^b tadpoles vs control	E, T	-, -	Brown et al. 2008
<i>Ranitomeya variabilis</i>	<i>Rhinella poeppigii</i> ^c chemical cues vs control	E	-	Schulte et al. 2011
	<i>Rhinella poeppigii</i> ^c chemical cues vs control	T	0	
<i>Ranitomeya variabilis</i>	<i>Ameerega trivittata</i> ^b chemical cues vs control	E, T	-, -	Schulte & Lötters 2014
	<i>Hylxalus azureiventria</i> ^c chemical cues vs control	E, T	-, -	
	<i>Hylxalus nexipus</i> ^c chemical cues vs control	E, T	-, -	
	<i>Osteocephalus mimeticus</i> ^c chemical cues vs control	E, T	-, +	

^a This study did not manipulate initial conditions (e.g. placement of eggs or tadpoles) at breeding sites but instead allowed for natural colonization.

^b *Ameerega trivittata* are herbivorous but were assumed to be perceived as potential predators based on morphological similarities to cannibalistic *Dendrobates*.

^c These species are omnivorous; they potentially consume eggs but do not consume live tadpoles.

^d Petranka et al. (1994) and Petranka and Holbrook (2006) were conducted in seminatural pools. All other studies were conducted using artificial pools placed in the field.

Table 2.3. Summary of **a)** experimental and **b)** correlational studies examining the effect of conspecific or heterospecific anuran presence (described as “explanatory variable” in Table **b**) on deposition site choice in anurans measured by # of eggs or egg masses deposited (E), tadpoles deposited (T), nests built (N), or ponds occupied (P). In Table **a**, – indicates avoidance of conspecifics or heterospecifics and 0 indicates no preference. In Table **b**, – indicates that species co-occurred less frequently than expected, + indicates that species co-occurred more frequently than expected, and 0 indicates no significant relationship.

a)

Species	Venue	Test performed	Variable measured	Response	Reference
<i>Bufo calamita</i>	Natural pools	Heterospecific eggs vs control	E	–	Banks & Beebee 1987
<i>Hyla chrysoscelis</i>	Artificial pools	Heterospecific tadpoles vs control	E	0	Resetarits & Wilbur 1989
<i>Hyla chrysoscelis</i>	Artificial pools	Conspecific tadpoles vs control	E	–	Resetarits & Wilbur 1989
<i>Aglyptodactylus laticeps</i>	Artificial pools	Conspecific tadpoles vs control	E	–	Glos et al. 2008
<i>Edalorhina perezii</i>	Artificial pools	Conspecific tadpoles vs control	E, N	–, –	Murphy 2003a
<i>Engystomops pustulosus</i>	Artificial pools	Conspecific nest vs control	N	–	Dillon & Fiaño 2000
<i>Engystomops pustulosus</i>	Natural pools	Conspecific nest vs control	N	0	Marsh & Borrell 2001

Table 2.3 b)

Species	Venue	Explanatory variable	Variable measured	Response	Reference
<i>Bufo b. spinosus</i>	Natural pools	heterospecifics	E, T	+, +	Indermaur et al. 2010
<i>Rana temporaria, Bufo bufo, Bombina variegata</i>	Natural pools	heterospecifics	T	+	van Buskirk 2005
<i>Scaphiopus couchii, Gastrophryne olivacea, Bufo speciosus, Bufo punctatus</i>	Natural pools	heterospecifics	T	–	Dayton & Fitzgerald 2001
<i>Melanophryniscus rubriventris</i>	Natural pools	conspecifics	E	0	Goldberg et al. 2006
<i>Edalorhina perezii</i>	Natural pools	conspecifics	N	–	Murphy 2003b
<i>Engystomops pustulosus</i>	Artificial pools	conspecifics	P	–	Marsh & Borrell 2001
	Natural pools	conspecifics	P	+	
<i>Engystomops pustulosus</i>	Natural pools	conspecifics	E, T	+, +	Rudolf & Rödel 2005
<i>Kuöixalus eiffingeri</i>	Natural pools	conspecifics	E	– (early season) / + (late season)	Lin et al. 2008

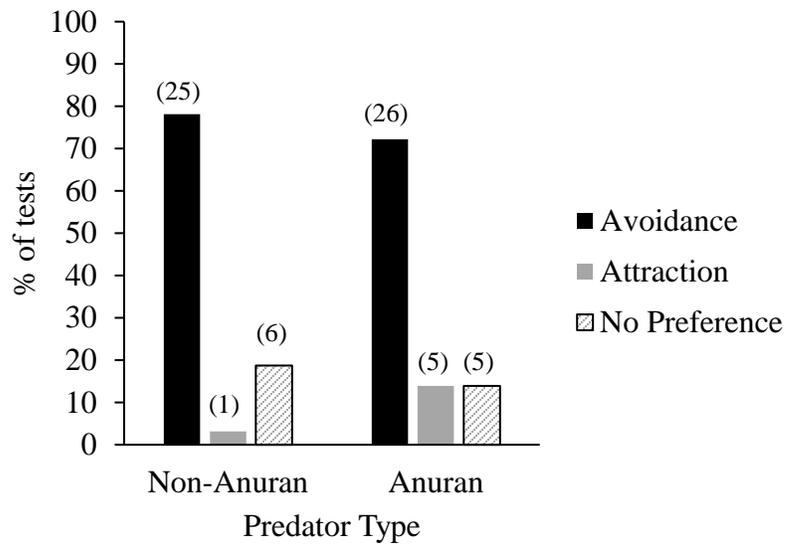


Figure 2. 1. Percent of published tests of anuran offspring deposition site selection behavior documenting avoidance, attraction, or no preference to sites containing non-anuran (i.e. fish, insects, shrimp, newts, salamanders, $n = 32$) and anuran predators ($n = 36$).

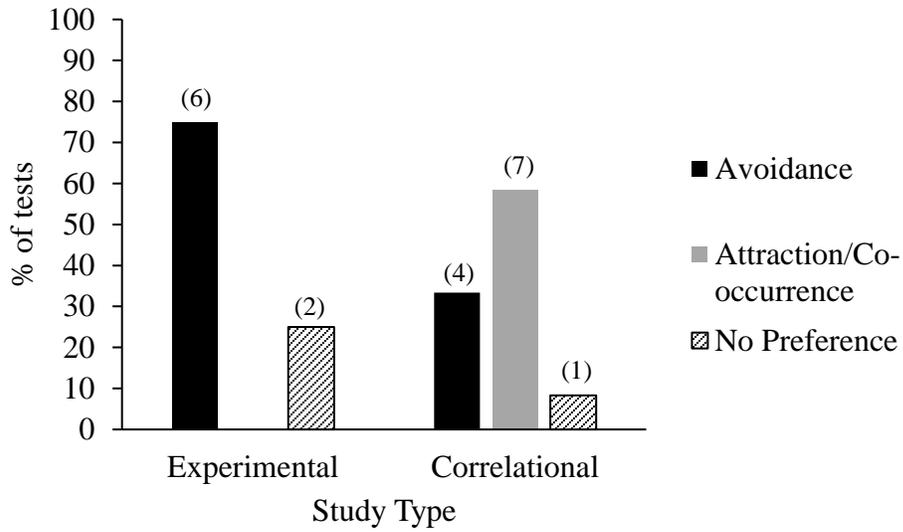


Figure 2. 2. Deposition site selection in relation to presence of conspecifics or heterospecific anurans. Response is indicated by avoidance of other anurans, attraction to (experimental tests) or co-occurrence with (correlational tests) other anurans, or no preference of habitat with other anurans.

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CHAPTER 3: USE OF CHORUS SOUNDS FOR LOCATION OF BREEDING HABITAT IN 2 SPECIES OF ANURAN AMPHIBIANS²

ABSTRACT

Conspecific cues have been shown to influence habitat selection in many different species. In anurans, conspecific chorus sounds may facilitate location of new breeding ponds, but direct experimental evidence supporting this notion is lacking. We conducted an experimental field study on American toads (*Anaxyrus americanus*) and Cope's gray treefrogs (*Hyla chrysoscelis*) to determine whether toads and treefrogs use acoustic cues to find new breeding areas by broadcasting chorus sounds at artificial ponds. We found that acoustic cues were effective in attracting *H. chrysoscelis* to ponds; playback ponds were detected by *H. chrysoscelis* at significantly faster rates and had greater rates of use than control ponds. *A. americanus* did not colonize ponds regardless of the presence of chorus sounds. This study provides some of the first experimental field evidence that anurans use conspecific cues to locate new breeding habitat, however species with certain life history traits may be more likely to exhibit this behavior. These findings may have valuable applications to amphibian conservation and management. If certain anuran species use presence of conspecifics to select habitat, managers may manipulate conspecific cues to passively translocate individuals across the landscape to target wetlands.

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INTRODUCTION

Social information, or information obtained from conspecifics or heterospecifics, can influence the decision-making process of individuals (Danchin et al. 2004). Individuals may rely on social information more often than they rely on their own personal experiences, particularly when direct sampling of the environment is a costly process in terms of both time and energy (Valone 2007). Using social information in the form of signals or other cues can reduce the uncertainty associated with decision-making; allowing individuals to quickly evaluate the environment and make informed decisions (Fletcher and Sieving 2010). These cues are typically acquired from conspecifics, as conspecifics share the same resource requirements, and therefore may provide valuable information regarding mate selection, foraging location, dispersal, and breeding habitat selection (Danchin et al. 2004, Seppänen et al. 2007).

In many taxa, dispersal and habitat selection are non-random, with animals using conspecific cues to locate and identify new, high-quality habitats (Fletcher and Sieving 2010). For example, juvenile *Anolis aeneus* lizards select territories previously occupied by conspecifics over equivalent, unoccupied territories (Stamps 1987) and salamanders select shelters marked with conspecific scent more often than unmarked shelters (Gautier et al. 2006). Harvestmen are attracted to new communal roosting locations based on the presence of conspecific chemical cues (Teng et al. 2012) and territorial songbirds use conspecific song to find suitable breeding habitat (Ward and Schlossberg 2004; Nocera et al. 2006; Hahn and Silverman 2007; Fletcher 2009). Anuran amphibians (i.e. frogs and toads) may also use conspecific cues to aid in dispersal and habitat selection, although there is currently little experimental evidence to support this notion.

Indeed, the mechanisms by which anurans locate new breeding ponds are poorly understood, although visual, olfactory, and acoustic cues have been suggested (Sinsch 1990). Previous research has primarily focused on how these cues affect homing and orientation to natal breeding areas (Grubb 1975; Sinsch 1987; Ishii et al. 1995; Pašukonis et al. 2014), with much less attention to how these cues operate in dispersal to new breeding ponds. Support for each of these mechanisms is lacking, and directed orientation towards a target using these mechanisms is thought to play only a minimal role in long-distance orientation of amphibians (Sinsch 2006). Current theory suggests that dispersers find distant new breeding ponds at random, as little evidence exists to suggest that individuals possess water-finding ability or the ability to use sounds of breeding choruses (Semlitsch 2008). However, if anurans do use specific cues, such as conspecific acoustic cues, to locate ponds, identifying these cues may have important implications for anuran ecology, conservation, and management.

If species select habitat based on the presence of conspecific acoustic cues, these cues may be manipulated to attract individuals to targeted areas. Such is the case with songbirds, where broadcasting playbacks of conspecific song in suitable but unoccupied habitats has been increasingly recognized as an effective, easy, and quick way to manipulate a species' presence or density in target locations and ultimately aid in management and conservation efforts (Ahlering et al. 2010; Ward et al. 2011). Although the use of acoustic attractants for management purposes has seldom been applied outside of birds, it may be a valuable tool in other species that communicate acoustically. For example, greater spear-nosed bats (*Phyllostomus hastatus*) are attracted to playbacks of conspecifics (Wilkinson and Boughman 1998), and based on that finding, it has been suggested that playbacks may be useful in attracting fishing bats (*Myotis vivesi*) to restored island habitats (Floyd et al. 2009). Similarly, playbacks may also be useful in

attracting anuran amphibians to restored habitats. Because anuran populations have been declining globally (Stuart et al. 2004), recent emphasis has been placed on the need to manage existing populations. Policies such as no-net-loss, which requires compensation for any damage or destruction to wetland habitat (Hough and Robertson 2008), create habitat for anurans. However, mitigation wetlands may suffer from poor colonization if anurans have no knowledge of this new habitat. If anurans do use acoustic conspecific cues to find new wetlands, then it may be possible for managers to assist in colonization or augmentation of targeted anuran species using playbacks.

Laboratory phonotaxis studies have repeatedly shown that anurans orient towards playbacks of conspecific individuals and choruses, however the majority of these studies have been investigated in the context of sexual signaling, with less attention to the role of chorusing in dispersal. Female American toads (*Anaxyrus americanus*), Cope's gray treefrogs (*Hyla chrysoscelis*), gray treefrogs (*Hyla versicolor*), barking treefrogs (*Hyla gratiosa*), and male wood frogs (*Rana sylvatica*) have all been found to approach recordings of a conspecific chorus, though green treefrogs (*Hyla cinera*) have been observed as unresponsive (Gerhardt and Klump 1988; Swanson et al. 2007; Bee 2007; Christie et al. 2010). These studies suggest that it may be beneficial for anurans to orient towards conspecific acoustic cues because such cues alert individuals to the timing and location of breeding aggregations and suitable habitat (Bee 2007), although the strength of response may be species specific. Additionally, because chorus sounds often propagate over several hundred meters in the natural environment, they provide a long-range cue to be exploited by any anurans in the area (Gerhardt and Klump 1988).

The chorus attraction hypothesis, reviewed in Gerhardt and Huber (2002), posits that anurans use conspecific choruses to locate new habitats. However, as they and others

acknowledge (e.g. Wells 2007), there has been little field evidence to support this hypothesis. Early, uncontrolled field studies placed chorus recordings of target frog and toad species on patches of dry land and found that individuals unfamiliar with the area (i.e. foreign, displaced frogs and toads) were found near the recordings (Oldham 1966, 1967). In an unpublished dissertation chapter, Martinez-Rivera (2008) also found evidence supporting the chorus attraction hypothesis with canyon treefrogs (*Hyla arenicolor*), but failed to find supporting evidence for bird-voiced treefrogs (*Hyla avivoca*), and suggested that these differential responses may be due to life history characteristics. *H. arenicolor* breed in unpredictable, ephemeral streams and have low philopatry, while *H. avivoca* breed in flooded forest and swamps and are highly philopatric, with little movement between breeding areas. Additional studies are necessary to determine if acoustic cues are used to locate breeding areas, how breeding ecology may affect acoustic cue use when dispersing, and whether manipulation of acoustic cues may be a valuable tool for managers.

We experimentally tested the chorus attraction hypothesis in a population of *A. americanus* and *H. chrysoscelis* in central Indiana using playbacks broadcast at newly installed artificial ponds. These species are common throughout eastern North America and exhibit similar tendencies to breed in a wide variety of habitats, although they exhibit different mating systems. *A. americanus* are typically explosive breeders, with peak reproductive activity generally lasting from less than a week to four weeks depending on location (Sullivan 1992, Pearman 1995). Explosive breeders may exhibit scramble competition where, in addition to calling to attract mates, males actively search for females (Wells 2007). In North Carolina, *A. americanus* has been observed breeding in small tire ruts and vernal pools, roadside ditches, farm ponds, lakes, and overflow pools along streams (Petranka et al. 1994, Pearman 1995), as well as

constructed wetlands in central Ohio (Porej and Hetherington 2005). *H. chrysoscelis* are prolonged breeders, with breeding lasting from two to four months throughout their range (Ritke et al. 1990). *H. chrysoscelis* exhibits a lek-like breeding system, where males call nightly from ponds and females choose males and initiate amplexus. *H. chrysoscelis* breeds in a variety of habitats including ephemeral wetlands, ponds, roadside ditches in Tennessee (Ritke et al. 1990), agricultural ponds in Minnesota (Knutson et al. 2004), and constructed wetlands in central Ohio (Porej and Hetherington 2005). In west central Indiana, Kolozsvary and Swihart (1999) observed *H. chrysoscelis*, as well as *A. americanus*, to be ubiquitous throughout their study site, and attributed this to the ability of both species to exploit a variety of wetland types for breeding. At our study area, we observed *A. americanus* explosively breeding in the permanent human-made pond, while *H. chrysoscelis* breeding took place over the course of three months in seasonal ponds.

We hypothesized that because *H. chrysoscelis* breed in habitat that may vary unpredictably, individuals may more readily rely on conspecific calls to locate potential breeding locations. Conversely, because *A. americanus* breed in more permanent wetlands, they may have higher site fidelity and thus may be less likely to use conspecific cues. Because *A. americanus* also have a short reproductive window, they may be more risk-averse to dispersing to an unknown location than are *H. chrysoscelis* that breed over a prolonged period. We therefore predicted that *H. chrysoscelis* and *A. americanus* should both colonize playback ponds faster and more often than control ponds, but *A. americanus* should exhibit less of a response to playbacks (i.e. fewer ponds colonized) than *H. chrysoscelis*.

METHODS

Study area

This study was conducted within a 44 ha forested area at the Camp Atterbury Joint Maneuver Training Center in central Indiana (39°19' N, 86°0' W). Bordering this area on the west side is a ~3 ha man-made pond that continually contains water and a 0.15 ha seasonal wetland, and bordering on the east side is a 0.20 ha seasonal wetland. In 2014, *A. americanus* were observed breeding in the human-made pond, but were not observed breeding in the seasonal wetlands, while *H. chrysoscelis* exhibited the opposite pattern. In March 2014 we installed 18 artificial garden ponds (1.7 m x 1.2 m, 91 gallon capacity) in a grid throughout the study area. Ponds consisted of a flexible polyethylene pond liner with two shallow shelves on each side (22.86 cm deep) and a deeper middle (45.72 cm deep). To install ponds, we used a tractor to dig out soil, and then placed ponds in the ground flush with the substrate. Ponds were separated from each other by ≥ 140 m to reduce the presence of acoustic cues from nearby playback ponds. We filled ponds with water from the nearby lake and placed leaf litter and braches in ponds to provide structural support for egg masses and facilitate growth of natural aquatic communities (i.e., providing a food source for any tadpoles in ponds).

Playback vocalizations

Beginning at the start of the *A. americanus* breeding season in April 2014 (prior to initiation of toad breeding) we broadcast prerecorded vocalizations of *A. americanus* at nine randomly selected artificial playback ponds (Fig. 3.1a). The remaining nine ponds were designated as silent controls. We used a random number generator to assign each pond to a particular treatment. Vocalizations were broadcast daily from approximately 1-2 h before sunset until midnight, with 15 minutes of silence after 60 minutes of calling to prevent habituation to playbacks. We broadcast vocalizations at volumes reflecting natural levels. We took sound pressure level readings of conspecific males calling from nearby locations and calibrated our

playbacks to reflect these levels using a Rion NA-27 sound level meter. Vocalization tracks consisted of 4 different exemplars obtained from recordings downloaded from the Macaulay Library (Macaulay Library, Cornell Lab of Ornithology). Exemplars contained calls of individuals and calls of a chorus, and did not contain heterospecific calls (see Appendix C for further details). Each exemplar was clipped to two minutes and repeated 6 times on a 60 minute track. When *A. americanus* were no longer heard calling from the natural surrounding ponds, we re-randomized playback and control locations and began broadcasting *H. chrysoscelis* calls (Fig. 3.1b). Similarly, vocalization tracks consisted of five different exemplars obtained from the Macaulay Library. We began broadcasting these calls at the end of April prior to when *H. chrysoscelis* were heard calling in the surrounding area. All playbacks were broadcast from a game caller (audio player within a speaker designed for attracting wildlife outdoors, FoxPro NX4) connected to a timer and powered by a deep-cycle battery. All materials were placed in a waterproof, camouflaged rubbermaid container located on the ground approximately 1.8 m from pond. Playbacks continued until mid-July, when treefrog calling in surrounding wetlands began to subside.

Field methods

To compare use of treatment versus control ponds, we evaluated latency to colonization (oviposition), number of oviposition events (egg masses), proportion of ponds with calling males, and capture rates at/near ponds. We checked ponds every 1-2 days, with a maximum of three days between checks, for evidence of oviposition events and, if egg masses were present, counted the number of masses in each pond. We removed any predators (excluding insects) observed in ponds such as crayfish or turtles. Once tadpoles reached Gosner Stage 41 (Gosner 1960), we batch marked tadpoles according to pond using visible implant elastomer injected in

the hindlimbs (VIE; Northwest Marine Technologies, Inc.). We opportunistically monitored ponds during evenings and nights for any anuran activity such as calling males and mating pairs. We captured and marked individuals seen at ponds using visible implant elastomer and visible alphanumeric tags (VIA; Northwest Marine Technologies, Inc.). We removed heterospecific males from playback ponds and returned these individuals to the human-made pond. We also removed conspecifics and heterospecifics (both males and females) from control ponds to ensure that the silent controls remained silent. Additionally, we conducted auditory surveys at surrounding natural ponds following the North American Amphibian Monitoring Program (NAAMP) protocol to determine relative abundance of each target species during their peak breeding period. NAAMP uses a calling index to quantify vocalization intensity, where a 1 indicates that individual calls can be counted without overlap, 2 indicates that individual calls can be counted but there is overlap, and 3 indicates that individual calls are continuous and overlapping (i.e. a full chorus; Weir et al. 2005).

Analysis

We used Fisher's exact test to determine whether colonization of ponds (via egg masses) was independent of treatment (playback or control). We examined relationships between treatment, pond colonization and distance to nearest wetland using logistic regression. We conducted a survival analysis, where survival time is defined as the time to when the first event occurs (i.e. first oviposition event; Johnson and Semlitsch 2003) and compared whether time-to-colonization curves differed between playback and control ponds using a log-rank test. We included ponds that were never colonized (i.e. an oviposition event had not occurred by the end of the study period) as censored in the survival analysis. We also calculated treefrog capture rate

(captures/night) at treatment and control ponds. All analyses were conducted in Program R (R Development Core Team 2010).

RESULTS

A. americanus were not attracted to newly created sites. None of the ponds (playback or control) contained egg masses and no *A. americanus* were observed at ponds during visual and auditory surveys. However, *A. americanus* were present in the area, with numerous toads (including calling males and mating pairs) observed at the nearby man-made pond located only 63 m from the nearest artificial pond. Auditory surveys conducted at the man-made pond for multiple nights during the peak toad breeding period (approximately a one week period in mid-April) yielded a call index of 3 on each occasion.

In contrast to *A. americanus*, we found strong support for the chorus attraction hypothesis in *H. chrysoscelis*. Oviposition events were observed in 7 of 9 (78%) playback ponds and 1 of 9 (11%) control ponds. Colonization of ponds was not independent of treatment, playback ponds were 21 times more likely to contain egg masses than silent control ponds ($p = 0.015$; Fig. 3.2). No relationship was found between distance to nearest wetland and treatment ($\beta = 0.002$, SE = 0.004, $p = 0.603$), and distance to nearest wetland and colonization probability ($\beta = -0.002$, SE = 0.004, $p = 0.547$). Time to colonization of ponds differed between treatments, with playback ponds significantly more likely to be colonized before controls ($\chi^2 = 7.9$, d.f. = 1, $p = 0.005$; Fig. 3.3). The first oviposition event occurred in a playback pond after 7 days of playbacks, while the first and only oviposition event occurred in a control pond after 28 days of playbacks. Additional oviposition events were subsequently observed in multiple playback ponds throughout the duration of the experiment, with one playback pond containing 9 oviposition events, each on different days.

During the experiment, we opportunistically observed males calling during the night at 9 of 9 playback ponds and 3 of 9 control ponds. Capture rate was 4.125 frogs per night at playback ponds and 0.186 frogs per night at control ponds. Male *H. chrysoscelis* were attracted to playback ponds relatively quickly, with calling males and a mating pair found at six playback ponds a week after the start of the experiment. In contrast, no calling males or mating pairs were observed at any control ponds until 25 days after initiation of experiment. During the experiment, we witnessed males consistently forming choruses at several different playback ponds. We observed that males would occasionally sit on top of playback bins, and would often time their calls to match the playbacks. Auditory call surveys of natural breeding ponds conducted throughout the peak breeding season (May-June) indicated that *H. chrysoscelis* were abundant in the area, with call surveys typically yielding index values of 3.

DISCUSSION

Our study provides some of the first rigorous field evidence supporting the chorus attraction hypothesis that anurans use acoustic signals to locate new breeding ponds. *H. chrysoscelis* exhibited strong conspecific attraction, finding and colonizing playback ponds faster and more often than controls, while *A. americanus* did not colonize any new ponds regardless of the presence of conspecific sounds.

We predicted that *H. chrysoscelis* would be more likely to use conspecific calls to find new habitats than *A. americanus* due to their breeding ecology. This is likely because there are differential costs and benefits associated with using cues for each species based on timing of breeding and breeding habitat. In our system, *A. americanus* were only observed breeding in the permanent pond, while *H. chrysoscelis* were only observed breeding in the seasonal ponds. Because *H. chrysoscelis* breed in habitats that may be more unpredictable in nature, they may

benefit from using conspecific acoustic cues to quickly locate breeding sites and aggregations, thereby reducing the time and energy spent searching for these resources. Anurans that breed in more stable water sources (e.g. *A. americanus*), on the other hand, may have little need to find new breeding sites and thus do not exhibit conspecific attraction. Because *A. americanus* were also explosive breeders in our system (we observed all breeding at the man-made pond occurring within a one-week span in mid-April), any prospecting of new and unknown breeding locations may put them at risk of missing their short reproductive window. *H. chrysoscelis*, however, are prolonged breeders and are less constrained by timing of breeding, and thus may be better suited to prospecting new habitat. Conspecific calls may serve as an indicator of habitat quality to these prospecting individuals (Ahlering et al. 2010), and, by selecting habitat containing conspecifics, individuals may reduce their risk of predation to themselves and offspring via the dilution effect (Ryan et al. 1981).

We acknowledge the possibility that lack of a response by *A. americanus* may be simply due to an aversion to our artificial ponds. However, based on a review of the literature, *A. americanus* breeds in a wide variety of habitats (e.g. shallow vernal pools to large lakes), thus we have no reason to expect that toads would avoid the ponds based on size. Additionally, the ponds used in this study were of similar depth to ponds preferred by *A. americanus* in Minnesota (0.5 m depth; Knutson et al. 2004). The ponds were also installed flush with the ground, with woody vegetation added to ponds so individuals would have no difficulty entering and exiting ponds. While it is possible that *A. americanus* were averse to using ponds used in this study based on some unknown factor associated with the structure or nature of the pond, we think it is unlikely.

An additional consideration not addressed in this study is whether *H. chrysoscelis* may exhibit attraction to any perceived noise, such as heterospecific calls, and not necessarily only

conspecific signals. Phonotaxis studies have shown that when an individual is presented with only a heterospecific call, some species will respond to these calls (Oldham and Gerhardt 1975, Ryan and Rand 1993, Bernal et al. 2007). However, when presented with both conspecific and heterospecific calls simultaneously, individuals typically orient towards the conspecific call (Kruse 1981, Ryan and Rand 1993, Pfennig et al. 2000, Bee 2007). Swanson et al. (2007) found that *A. americanus* females oriented towards artificial chorus-shaped noise in the phonotaxis arena, while *H. chrysoscelis* females only oriented towards natural chorus noises, suggesting that toads may be less selective to a stimulus. Orienting towards any perceived signal, including a heterospecific signal, would appear to be costly in terms of time and energy and ultimately result in incorrect or failed mating opportunities (Bernal et al. 2007). It has been suggested that anurans may only orient towards heterospecific calls if conspecific calls are scarce in the landscape, and if heterospecific calls share similar key features with conspecific calls (Wells 2007). However, future work should consider the issue of a silent control, and perhaps use artificial chorus-shaped noise or similar heterospecific calls to ensure that individuals are not orienting towards any perceived sound. In our study, we did not observe species other than *H. chrysoscelis* at our ponds, despite the presence of cricket frogs (*Acris crepitans*), green frogs (*Lithobates clamitans*), and bullfrogs (*Lithobates catesbeianus*) breeding concurrently in nearby natural breeding areas.

Previous work investigating the function of chorus sounds have largely been examined in the context of sexual selection, with little attention to how chorus sounds might affect dispersal and habitat selection. This is surprising, given that dispersal to new breeding ponds is a major process in the anuran life cycle and governs both population regulation and metapopulation dynamics (Semlitsch 2008). Here we see that chorus sounds play a significant role in this important anuran life process. A variety of mechanisms have been suggested for anuran location

of new breeding ponds including visual, olfactory and acoustic (Sinsch 1990), and our results provide clear evidence for an acoustic mechanism, in the form of conspecific cues, for dispersing *H. chrysofelis*. Because our treatment and control ponds presented similar visual and olfactory cues, our results suggest that acoustic cues can be used independently of other cues. Indeed, it is likely that visual cues have limited use and are employable only at short ranges, particularly because amphibians typically travel to breeding habitat at night. Olfactory pond cues may be used for orientation at longer distances (Oldham 1967, Sinsch 1987), although rigorous field evidence on the distance at which anurans can detect and use pond olfactory cues is lacking. Regardless, in our study acoustic cues appear to be the primary cue used to find new ponds at longer distances.

Because this is one of the first studies on chorus sound use and anuran habitat selection, there are many more questions to address. Our study was not able to address the spatial scale at which *H. chrysofelis* use calls to locate breeding ponds. Because we did not know the initial starting point of *H. chrysofelis* in the landscape, we could not determine distances at which treefrogs use acoustic call to orient. Swanson et al. (2007) reported that female *H. chrysofelis* oriented to chorus sounds in a phonotactic arena up to a distance of 40 m, but did not orient at 80 or 160 m. Similarly, Christie et al. (2010) found that female *H. versicolor* oriented to chorus sounds in a phonotactic arena up to 32 m, but did not orient at 50 or 100 m. The distance at which frogs are able to detect auditory cues depends on both the treefrog auditory system as well as the propagation and attenuation of acoustic signals in the landscape. More targeted work in this area would be necessary to clarify the spatial scale of acoustic cue use in *H. chrysofelis*.

In this study, we varied density of calling males on our recordings because we were unsure of which group size would attract the largest number of individuals. While previous

research has shown that number of males and females at a pond are correlated (Ryan et al. 1981, Dyson et al. 1992), it is still unclear whether individuals are actually attracted to larger groups. For females, advantages to selecting larger groups may include increased female mate choice and greater protection from predation (Ryan et al. 1981). For males, advantages may similarly include reduced risk of predation, as well as an opportunity to exploit the advertisement calls of more attractive males (Beehler and Foster 1988). Conversely, female risk of unsolicited matings may increase with larger group size, and ability to discriminate among males may be reduced (i.e. greater masking interference; Gerhardt and Huber 2002). Few studies have experimentally examined the relationship between group size and attraction in anurans, although Murphy (2003) found that experimentally reducing the number of calling males at a pond had no effect on female or male visitation rates, suggesting that females may not be attracted to larger groups. While our goal in this study was not to investigate how density dependence influences habitat selection, we recommend that further work be done regarding chorus size and attraction, and how other factors (e.g. distance to signal) may influence this relationship.

While we have shown that *H. chrysoscelis* can use acoustic signals to find new breeding habitats and colonies, it is still unclear how an initial colonist finds an unoccupied habitat and why that individual subsequently decides to settle there. The discovery of unoccupied habitat may indeed be a random process, whereby a dispersing individual inadvertently encounters new habitat (Semlitsch 2008). The individual may then decide to settle at the habitat based on specific vegetation features or pond characteristics. For example, natterjack toads (*Bufo calamita*) seek out ponds with specific physical and chemical properties (Banks and Beebee 1987), wood frogs (*Lithobates sylvaticus*) prefer to breed in fish-free ponds (Hiopey and Petranka 1994), and mountain chorus frogs (*Psuedacris brachyphona*) preferentially select breeding ponds within

forested areas (Felix et al. 2010). While species-specific habitat preferences are well documented, many questions still remain on anuran movement to new ponds.

In addition to providing evidence for the chorus attraction hypothesis, we also provide insights into the movements of *H. chrysofelis* during the breeding season. In particular, our study demonstrates much greater use of terrestrial habitats during the breeding season than has been previously documented. In a study of breeding season terrestrial habitat use by *H. versicolor*, Johnson et al. (2007) found that females on average were located 80 m from breeding sites while males were located 30 m, indicating that it is not uncommon for treefrogs to make short-distance forays into terrestrial habitat. We found *H. chrysofelis* and reproductive activity at artificial ponds located up to 345 m from natural treefrog breeding areas, and also observed that the pond with the highest number of oviposition events was located 261 m from the closest natural treefrog breeding pond. Johnson and Semlitsch (2003) similarly placed artificial ponds at distances of up to 200 m from natural breeding areas into terrestrial habitat and found that 95% of gray treefrog breeding activity occurred in artificial ponds within 15 m of the natural breeding pond. This result is likely due to the lack of social cues at distant breeding ponds, leading to decreasing probability of colonization as distances from natural breeding ponds increased. However in our study there was no relationship between colonization probability and distance from natural breeding pond, distant ponds were equally likely to be colonized as ponds close to the natural breeding pond. This suggests that if there is a cue present for frogs to find new breeding ponds, then inter-pond distance may not represent as significant of a barrier to colonization than previously perceived. Thus our study demonstrates that *H. chrysofelis* readily prospect new breeding areas and may make long distance movements through terrestrial habitat.

However, we do note that our study area was completely forested and conducive to treefrog movement.

Conservation Implications

The use of conspecific cues by anurans has important implications to amphibian management and conservation. Using playback systems, we were able to attract *H. chrysoscelis* to new breeding areas. This discovery may be especially useful to managers seeking to restore or augment amphibian populations at newly created or restored wetlands. Although we were unable to attract *A. americanus*, we expect that this lack of response may be context dependent and that *A. americanus* may be more responsive in areas without permanent wetlands. Playback systems are relatively inexpensive and easy to construct, and require little maintenance effort. Playbacks have been used successfully in attracting several species of songbirds (including certain endangered species; Ward and Schlossberg 2004) to unoccupied but suitable habitat, and are now a valuable tool in avian management and conservation (Ahlering et al. 2010). While we have only reported on the efficacy of playbacks for *A. americanus* and *H. chrysoscelis*, we expect that anuran species with comparable breeding ecologies to *H. chrysoscelis* may respond similarly to conspecific calls. Because of the dubious track record associated with current amphibian management solutions, such as translocation, there is a need to evaluate other alternatives (Germano and Bishop 2009). We believe that playbacks may be a promising method by which managers can passively move amphibians, including threatened or endangered species, across the landscape to new breeding areas.

FIGURES

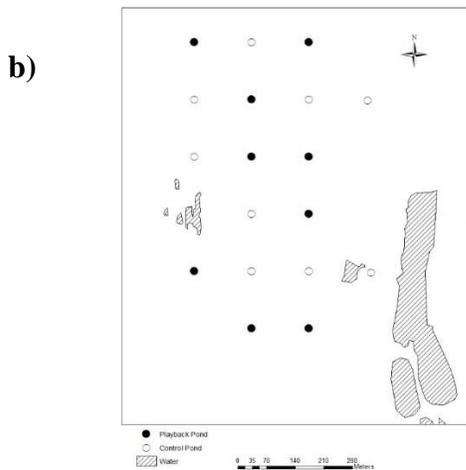
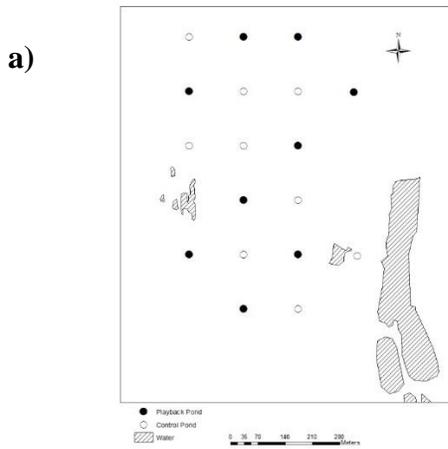


Fig 3.1. Locations of experimental ponds at Camp Atterbury Joint Manuever Training Center in central Indiana for **a)** *Anaxyrus americanus* and **b)** *Hyla chrysoscelis*. Black circles indicate treatment ponds with conspecific playback and white circles indicate silent control ponds.

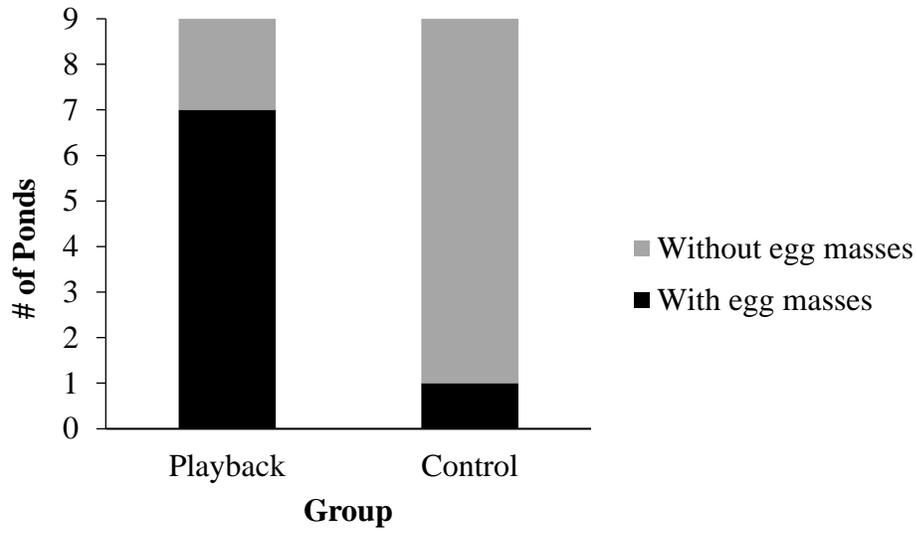


Fig 3.2. Number of playback and control ponds found with egg masses for *Hyla chysoscelis*.

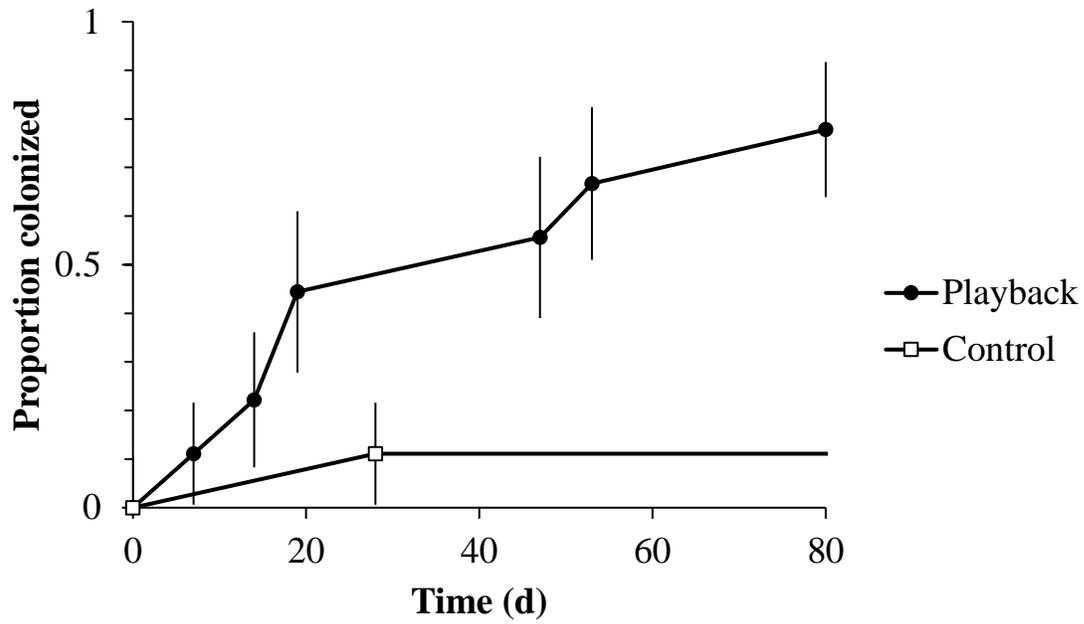


Fig 3.3. Time in days (d) until first colonization (i.e. oviposition event) of ponds by *Hyla chrysoscelis* represented by survival curves. Each point represents an initial oviposition event with associated standard error bars.

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CHAPTER 4: CHORUS SOUNDS FACILITATE CONSPECIFIC ATTRACTION FOR CERTAIN SPECIES OF ANURAN³

ABSTRACT

Many organisms, including species of songbird, anole, salamander, and spider, use conspecific social information in the habitat selection process. Less is known, however, regarding the importance of conspecific cues, such as chorus sounds, in facilitating location of and aggregation at breeding habitats in anuran amphibians. Presumably, importance of cues varies by species' breeding ecology and environmental characteristics. We investigated responsiveness to chorus sounds in seven species of anurans across three field sites during 2014-2016. For each species, we broadcast conspecific chorus sounds at artificial pools and recorded colonization at each pool. We compared differences in number of pools found with egg masses between playback and control pools and examined latency to first colonization. We found that seasonal or temporary pond breeders were more likely to respond to calls than permanent pond breeders. We discuss potential mechanisms behind these differences and the implications for amphibian management and conservation.

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INTRODUCTION

Social information is used by a wide variety of organisms to reduce uncertainty inherent in the natural environment (Danchin et al. 2004). This uncertainty may be related to decisions regarding habitat selection, dispersal, mate quality, resource availability, or predation risk (Blanchet et al. 2010). By observing how others interact with and behave in the environment, individuals can acquire information to make better informed decisions that should ultimately increase survival, reproductive success, and fitness (Miller et al. 2013). For example, nine-spined sticklebacks (*Pungitius pungitius*) use foraging rates of conspecifics to decide in which patch to forage (Coolen et al. 2003), black-legged kittiwakes (*Rissa tridactyla*) use reproductive success of neighbors to decide whether to disperse or remain in the patch (Boulinier et al. 2008), and fruitfly females (*Drosophila melanogaster*) decide which males to mate with based on the mating decisions of conspecific females (Mery et al. 2009).

In the case of habitat selection, individuals may use conspecific presence or abundance as positive proximate cues when deciding where to settle (Fletcher 2006). This phenomenon, known as conspecific attraction, results in individuals of the same species settling or aggregating near each other (Stamps 1987). The mechanisms for conspecific attraction are not thoroughly understood, but likely include location of habitat and indirect assessment of habitat quality (Valone and Templeton 2002). Thus, rather than personally searching and sampling multiple sites, an individual could use conspecific location cues to quickly locate high-quality habitat (Valone 2007). Many species use conspecific cues when locating or selecting habitat, including common noctule bats (*Nyctalus noctula*; Furmankiewicz et al. 2011), orb-weaving spiders (*Nephilengys cruentata*; Schuck-Paim and Alonso 2001), bronze anoles (*Anolis aeneus*; Stamps 1988), and Luschan's salamanders (*Mertensiella luschani*; Gautier et al. 2006). In addition,

conspecific attraction occurs frequently in breeding birds, and several studies have experimentally demonstrated that birds can be attracted to areas containing conspecific vocalizations (Ahlering et al. 2010). Responsiveness to conspecific information may vary by avian species however, with Ahlering et al. (2010) positing that species most likely to exhibit attraction are those with aggregated territories or patchy distributions, a large juvenile to adult ratio, few breeding opportunities, migratory tendencies, and a short or asynchronous breeding season.

Interestingly, many anuran species share the same characteristics with avian species as listed above. During their relatively short breeding season, anurans migrate to centralized locations where males produce calls to attract females that often propagate at long ranges in the environment (Gerhardt and Klump 1988). Anurans typically have few opportunities to breed, and when they do, produce large numbers of young. Seemingly, such characteristics might predispose anurans to conspecific attraction and using conspecific calls as location cues (Nocera et al. 2006). Surprisingly, however, the role of conspecific cues in facilitating aggregation of anuran amphibians is unknown and field evidence on the topic is scarce (Gerhardt and Huber 2002, Gerhardt and Bee 2007). Several decades ago, Oldham (1967) found that green frogs (*Lithobates clamitans*) transplanted to a foreign location were more likely to orient towards conspecific calls than were local frogs. More recently, James et al. (2015) found that conspecific call playbacks influenced the within-pond distributions of green and golden bell frogs (*Litoria aurea*). Results from laboratory studies are more promising; male wood frogs (*Lithobates sylvaticus*), female barking treefrogs (*Hyla gratiosa*), female gray treefrogs (*Hyla versicolor* and *Hyla chrysoscelis*), and female American toads (*Anaxyrus americanus*) will orient towards chorus sounds emanating from a speaker (Bee 2007, Gerhardt and Klump 1988, Swanson et al.

2007, Christie et al. 2010). If anurans do use conspecific cues such as chorus sounds in a natural environment, then managers could use this technique to enhance colonization of newly created or restored wetlands (Buxton et al. 2015).

For anurans, use of cues and efficacy of conspecific attraction as a management tool may potentially vary by characteristics of both the species life history and its environment. For example, breeding season length may influence responsiveness in which species with short breeding windows (i.e. explosive breeders) might use conspecific cues to more quickly locate breeding habitat (Nocera et al. 2006). However, species with longer breeding windows (i.e. prolonged breeders) might also be prone to using social information if late-arriving individuals use cues of early arriving individuals to find habitat (Ahlering et al. 2010). Breeding pond habitat use may also influence social information use such that species breeding in temporally or spatially unpredictable ponds might be more likely to exploit conspecific cues than those breeding in reliable water bodies (i.e. permanent ponds; Bee 2007). Finally, local or regional environmental characteristics might influence conspecific attraction. In dry climates where rainfall occurs sporadically and breeding ponds are scarce and isolated, anurans may use conspecific cues to quickly locate suitable habitat and reduce search costs (e.g. desiccation risk, predation risk). Collectively, any of the above-mentioned factors might interact to influence a species' tendency to use social information and exhibit conspecific attraction.

We experimentally examined conspecific attraction in seven species of anuran amphibians at three field sites located in Illinois, Indiana, and Arizona. Selected species occurred in areas with and without significant predictable precipitation and encompassed a variety of life history characteristics and breeding strategies. In 2014, we tested American toads, Cope's gray treefrogs, and green frogs. In 2015, we tested wood frogs, spring peepers (*Pseudacris crucifer*),

Cope's gray treefrogs, and green frogs. In 2016, we tested Mexican spadefoots (*Spea multiplicata*) and Arizona treefrogs (*Hyla wrightorum*). For each species, we broadcast playbacks of conspecific calls at artificial ponds throughout the breeding season. We monitored subsequent colonization of ponds through egg mass counts and determined whether treatment (i.e. playback) ponds were colonized significantly more often than control (i.e. silent) ponds.

MATERIALS AND METHODS

Study species

We selected species that encompassed a range of life-history characteristics (Table 4.1). Cope's gray treefrogs, spring peepers, and green frogs are prolonged breeders, while the remaining species tend to be more explosive in our study areas. Green frogs and American toads bred in more permanent ponds, while the other species bred in a variety of habitats. Arizona treefrogs and Mexican spadefoots were limited to the southwestern United States and Mexico, while the rest of our species were relatively widespread throughout the eastern United States and North America (Dodd 2013).

Study Sites and Experimental Design

Indiana

We tested conspecific attraction in Cope's gray treefrogs and American toads in 2014 and wood frogs in 2015 at Camp Atterbury Joint Manuever Training Center in central Indiana. The study site was located in a forested area containing several seasonal wetlands, as well as a human-made permanent pond. Auditory surveys in 2014 indicated that treefrogs and wood frogs bred primarily in the seasonal wetlands, whereas toads bred only in the human-made permanent pond. In March 2014, we installed 18 artificial garden ponds (1.7 m x 1.2 m, 344 L capacity, Lowe's model # FPSK91) 140 m apart from each other in a grid throughout the study site. Ponds

were made of flexible polyethelene liner and had two shallow shelves on each side (22.86 cm deep) and a deeper middle (45.72 cm deep). We placed ponds flush with the ground and filled them with water from nearby wetlands as well as leaf litter and branches to facilitate growth of aquatic communities and provided structural support for egg masses.

For each species, we randomly designated ponds as either playback or control. Playbacks consisted of a callbox (FoxPro NX4) broadcasting conspecific vocalizations while controls were silent. Soundtracks of recordings consisted of 4-5 different exemplars obtained from publically available or commercial sources. Each exemplar was 2 minutes long and repeated multiple times on a 60-minute track. After 60 minutes of playbacks, 15 minutes of silence was interjected to prevent attenuation. Exemplars for each species only contained conspecific calls and consisted of both individual calls and calls forming a chorus. Callboxes were connected to a timer and deep cycle battery contained within a waterproof plastic bin placed approximately 1.8 m from the pond. We began broadcasting calls at playback ponds prior to the start of each species' respective breeding periods at times when the species would naturally be calling in the surrounding environment and at volumes reflecting natural levels (Table 4.2). In 2014 after American toad breeding subsided, we re-randomized pond treatments for Cope's gray treefrogs. We again randomized treatment for wood frogs in 2015. We stopped playbacks for each species after breeding and calling in the surrounding environment had abated.

Illinois

We tested Cope's gray treefrogs and green frogs in 2014 and again tested those two species as well as spring peepers in 2015 at Sparta Training Area in southern Illinois. Ponds were installed in late May 2014 in a grassy matrix with interspersed shrubs surrounded by permanent constructed lakes and ponds. Because of logistical constraints, 8 ponds were placed in the

northern section of the site and the remaining ten ponds were placed >1500 m away in the southern section. Ponds were located in a grid 200 m apart from each other and were identical to the ponds described above. In 2014, we randomized treatment between northern and southern pond locations and began playbacks for target species despite natural calling and breeding commencement several weeks prior. We jointly targeted gray treefrogs and green frogs using alternating playbacks at treatment ponds during times when species' were naturally calling (Table 4.2). We used 4-5 exemplars for each species and broadcast calls for each species for four minutes before alternating to the other species. After 60 minutes of playbacks, we interjected 15 minutes of silence to prevent attenuation. We ceased calls in 2014 when natural calling by target species had begun to subside. In 2015, we re-randomized treatment locations and targeted spring peepers beginning in early March using the same methods as above. When the treefrog breeding season was nearing, we switched playbacks to alternating spring peeper and treefrog calls. Later in the spring, we again switched playbacks to alternating treefrog and green frog calls. We did not re-randomize treatment during these switches. Calls were stopped when breeding and calling in the surrounding environment had subsided.

Arizona

We tested two species, Arizona treefrogs and Mexican spadefoots, for conspecific attraction in 2016 on United States Forest Service property in southeastern Arizona. Anuran surveys in 2015 confirmed that both of these species were present on the property. We tested treefrogs at Brown Canyon Ranch (BCR), a public use area with two constructed permanent ponds. We tested spadefoots at a separate site closed to the public (hereafter referred to as "admin site") that contained one constructed temporary pond and one constructed permanent pond. Both sites consisted of desert grassland and shrubs. In late June 2016, we installed 16

plastic ponds (i.e. child-size wading pools) at BCR and 14 ponds at the admin site. Ponds were located ≥ 70 m apart from one another and were placed at varying distances from the source pond. Ponds were 1.14 m in diameter and were filled with approximately 94 L of water from one of the nearby existing ponds. Ponds were placed on the ground rather than flush with the ground because the desert soil did not permit easy digging. We piled up rocks in two separate locations on the inside and outside of the pond so anurans could enter and exit. We placed sticks and vegetation in ponds for structural support for egg masses. At each site, we randomly designated treatment and control ponds while accounting for distance to nearest natural water source. Prior to the start of the breeding season, we began broadcasting calls for each target species at treatment ponds (Table 4.2). Similar to the methods described previously, we used 4 exemplars for each species (including both commercially available recordings and recordings made by the author VLB at the site in 2015) and broadcast calls at times when each species would naturally be calling.

Monitoring and Data Analysis

To determine the effect of playbacks on anuran behavior, we monitored all ponds every 1-3 days for egg masses. If masses were present, we counted the number of eggs and egg masses in each pond. At the Arizona field sites we relocated any eggs found in our ponds to nearby source breeding pools after counting. We did this because our ponds were small and had limited food resources. Additionally, we considered that high larval densities in pools could deter individuals from breeding in that pool. At each field site, we opportunistically conducted night surveys for evidence of calling males and reproductive activity. In Arizona, we randomly placed auditory recorders (Song Meter SM4; Wildlife Acoustics, Inc.) at our experimental ponds (both playbacks and controls) to further determine whether any frog activity was occurring.

We performed Fisher's exact tests for those species that colonized ponds to examine the relationship between pond colonization and treatment. We examined whether distance to nearest water source influenced pond colonization using logistic regression. For those species with multiple colonization events, we conducted a survival analysis and log-rank test to determine whether there was any difference in time to first colonization between playback and control ponds.

RESULTS

Cope's gray treefrogs (in Indiana only) and Mexican spadefoots were more likely to oviposit in playback ponds compared to control ponds, but there was weak or no evidence of an effect of playbacks on colonization by the remaining species (Fig. 4.1, Table 4.3). Latency to initial pool colonization for both species indicated playback ponds were more likely to be colonized before control ponds (gray treefrog: $\chi^2 = 7.9$, $df = 1$, $P = 0.005$, Fig. 4.2a; spadefoot: $\chi^2 = 5.2$, $df = 1$, $P = 0.023$, Fig. 4.2b) and multiple playback ponds subsequently received additional oviposition events throughout the experiment. For both species, colonization probability was not associated with distance to nearest existing breeding wetland (gray treefrogs: $\beta = -0.003$, $SE = 0.004$, $P = 0.517$; spadefoots: $\beta = -0.017$, $SE = 0.011$, $P = 0.134$).

The remaining species either had a weak response to the playback or did not colonize the ponds at all. For Arizona treefrogs, only one pond (a playback pond) was colonized. This pond was one of two playback ponds nearest to the pre-existing breeding pond and was colonized on the second night after natural calling had started at the existing pond. For wood frogs, slightly more treatment ponds were colonized than control (6 versus 4), but this difference was not significant and the first two ponds colonized were control ponds (Fig. 4.2c). For Cope's gray treefrogs in Illinois, equivalent numbers of playback and control ponds were colonized. No

playback or control ponds were found with egg masses for green frogs, spring peepers, and American toads.

Opportunistic visual and auditory surveys revealed that adult use of ponds varied by species. In Indiana, throughout the experiment we observed treefrog males calling at 9 of 9 playback ponds and 3 of 9 control ponds, whereas in Illinois in 2015 we only observed treefrog adults at 3 of 9 playback ponds and 1 of 9 controls (Table 4.3). For the explosive-breeding wood frogs, on the first day of breeding activity we found adults in 7 of 9 playback ponds and 2 of 9 controls. On the second day of breeding, we found adults in 8 playback ponds and 7 controls. After the third day, the number of ponds with adults began to decline for both treatment and control as breeding activity in the surrounding environment subsided. Surveys for spadefoots, as well as the opportunistic placement of frog loggers at our experimental ponds, found calling males at 5 of 7 playback ponds and 1 of 7 control ponds, and found that males called at playback ponds in response to playbacks even when no natural calling or breeding was taking place in the surrounding landscape.

DISCUSSION

Our study demonstrated a strong response to conspecific playbacks by Cope's gray treefrogs and spadefoots, but weak or no response to playbacks by wood frogs, American toads, Arizona treefrogs, spring peepers, and green frogs. Based on laboratory experiments, Cope's gray treefrogs, Mexican spadefoots, wood frogs, and American toads had been hypothesized to use conspecific calls in the context of conspecific attraction (Pfennig et al. 2000, Bee 2007, Swanson et al. 2007), but until this point, little field validation existed. We had expected that differences in responsiveness would be attributed to variation in species breeding ecology, habitat use, or landscape characteristics, but we unveiled few consistent patterns. For anuran

amphibians, the costs and benefits of using location cues for conspecific attraction are likely more extreme than for other taxa (e.g. birds) because of their limited mobility and dispersal abilities, physiological constraints, and, in some cases, brevity of breeding period. While our results answer a previously unresolved question on species use of conspecific chorus sounds to facilitate aggregation at new breeding ponds, a number of new questions have emerged.

In our study, breeding pond habitat type appeared to influence use of social information, with those species using seasonal or ephemeral ponds more likely to respond to playbacks. We saw no use of our experimental ponds by permanent pond breeding American toads and green frogs. While the lack of a response by green frogs could potentially be due to low densities at our site, toads were abundant. For most permanent pond breeders, there may be little benefit to using calls to locate alternate breeding areas because they already have personal information on a stable, reliable water source. In contrast, seasonal and temporary pond breeders, such as gray treefrogs and Mexican spadefoots, may use calls to locate breeding aggregations that vary unpredictably (Bee 2007). Gerhardt and Klump (1988) similarly concluded that barking treefrogs responded to conspecific chorus sounds in the laboratory while green treefrogs did not because of their differing breeding habits; barking treefrog aggregations are spatially and temporally unpredictable while green treefrog aggregations are more stable in space in time. Correspondingly, avian conspecific attraction studies have found that species using more ephemeral breeding habitats are strongly attracted to conspecific location cues prior to the breeding season (Ward et al. 2011).

In addition to habitat, social information use may also be influenced by duration of breeding. A prolonged breeding period, exhibited by gray treefrogs, potentially allows late-arriving individuals to cue in on the calls of early-arrivers and increases the amount of time

available for individuals to prospect multiple breeding sites without losing out on many potential breeding opportunities (Ward 2005, Aherling et al. 2010). At our study site in Indiana, treefrogs were significantly more likely to colonize playback ponds, and we observed treefrogs arriving at these ponds throughout the breeding season. Arguably, explosive breeding might also select for social information use because individuals need to quickly locate breeding habitat and aggregations (Bee 2007). However, we saw that explosive breeding American toads and wood frogs did not show a strong response to playbacks. We expect that lack of a response by toads was associated with their use of only the permanent pond for breeding. Prospecting new breeding sites when there was already a stable and predictable breeding area available may have been too risky for a population with a three-day breeding window. Wood frogs bred explosively in seasonal wetlands on site, and while there appeared to be a response to playbacks by adults migrating to breeding ponds on the first day of breeding activity (almost four times as many playback ponds were found with adults compared to controls), this effect dissipated by the second day. The explanation behind this observation is unclear, but wood frog adults appear to readily colonize new ponds and the high numbers of wood frogs present at our site may have increased the chances of individuals randomly encountering any of our ponds. Further, conspecific attraction via social cues may be ineffective at high population densities because of increased competition costs (Fletcher 2007).

Mexican spadefoots and Arizona treefrogs both bred explosively but differed in their responsiveness to playbacks, with spadefoots colonizing over half of the playback ponds and treefrogs only colonizing a single playback pond. For desert-dwelling species, orientation using conspecific calls would seem particularly valuable because random movement in search of breeding ponds can be very risky in xeric habitat. However, differences in breeding habitat use

as well as species physiology may have contributed to responsiveness to conspecific calls. Arizona treefrogs generally use more permanent water bodies and are more desiccation prone and less mobile compared to spadefoots, which may decrease willingness to engage in exploratory behavior and increase fidelity to isolated perennial pools (Mims et al. 2016). Interestingly, Mims et al. (2015, 2016) found that Arizona treefrogs in the same region had greater genetic differentiation among breeding sites than spadefoots, with physical distance as the main driver of genetic distance. This outcome suggests that dispersal ability of treefrogs is likely limited. In our study, the only pond found with treefrog eggs was one of the playback ponds closest to the source breeding pond (98 m) while a control pond located 45 m from the source pond was not colonized.

Notably, playbacks appeared to extend the breeding season of spadefoots at our site. We observed calling males and breeding activity at our playback ponds even on nights when no natural chorus formed. While breeding activity typically occurs only after torrential rainfall (Dodd 2013), we found egg masses in a playback pond at least three weeks prior to the first major breeding bout before the temporary pond had filled up with water. Martinez-Riveria (2008) similarly found that bird-voiced treefrog males (*Hyla avivoca*) exposed to playbacks before the onset of the breeding season and before daily chorus formation moved to chorus sites earlier and formed a chorus whereas males in control sites without playbacks showed no similar behavior.

Interestingly, we observed within-species differences for gray treefrogs between our sites, potentially related to landscape characteristics of each site. In Indiana, ponds were within a forested matrix and gray treefrogs responded strongly to playbacks. In Illinois, ponds were located primarily in a grassy matrix and there was no difference in colonization rates between

playback and control ponds. Previous research has found that ponds located increasingly further from forest edges are less likely to be colonized by gray treefrogs (Hocking and Semlitsch 2007), thus treefrogs in Illinois may have been unwilling to venture away from treelines. The forested nature of the Indiana site likely also facilitated movement between ponds and decreased risk of predation and desiccation. We also note that abundance issues may have led to lack of colonization in Illinois, as treefrogs were much more localized at this site and were never heard calling in the area where the northern ponds were located. Additionally, the alternating green frog calls at playback ponds could have deterred individuals from using ponds, but we think it is unlikely. Resetarits and Wilbur (1989) suggested that breeding Cope's gray treefrogs did not avoid bullfrog larvae (*Lithobates catesbeiana*) because the two species do not generally use the same habitats. Similarly, in our study area green frogs and treefrogs do not generally share habitats which, combined with the low densities of green frogs at the site, probably results in little selection pressure for avoidance. Interestingly, we note that many other studies have found gray treefrogs responsive to playbacks, and they are generally considered a model organism for phonotaxis studies (Bee 2015). Thus, the general responsiveness of treefrogs observed here may be attributed to some underlying characteristic of their physiology rather than their breeding ecology.

Our results demonstrate that conspecific attraction via conspecific vocalizations is only likely to occur under a particular set of circumstances. In some cases, the costs of using social information appear to outweigh any potential benefits. For those individuals that already have reliable personal information on breeding location (e.g. permanent pond breeders), prospecting new sites may yield little benefit, especially if the breeding window is short. However, for individuals that breed in more hostile landscapes (e.g. desert-dwelling species), using conspecific

cues to guide migration to ephemeral breeding ponds may be less risky than a random search strategy. Fletcher (2006) demonstrated that survival increases if individuals use social cues to find habitat in a hostile matrix rather than randomly searching. Costs and benefits to using social information may also be regulated by a variety of other factors including degree of habitat fragmentation (Albrecht-Mallinger and Bulluck 2016) conspecific density (Fletcher 2007), species physiology (e.g. desiccation tolerance), and individual age (Ward and Schlossberg 2004, Nocera et al. 2006). In birds, juveniles and first time breeders tend to use social information more than adults, presumably because they have no prior information suitable habitat (Ahlering et al. 2010). While our study did not examine in detail the relationship between social information use and each of the aforementioned factors, we expect that future research on this topic will clarify when it may be advantageous for anurans to use conspecific cues.

An understanding of the role of social cues in the habitat selection process by anurans may have important ramifications for conservation and management (James et al. 2015). If species use social cues to find breeding habitat, restored or mitigated wetlands may go uncolonized if proper social cues are not provided (Ahlering and Faaborg 2006). Indeed, avoidance of high-quality areas based on missing or unattractive selection cues is often referred to as a “perceptual trap” and could ultimately constrain successful restoration (Patten and Kelly 2010, Hale and Swearer 2016). Consequently, providing social cues may facilitate dispersal to new sites and potentially re-establish connectivity among ponds on a larger landscape-level scale (James et al. 2015). In already occupied areas, chorus sounds may help augment existing population sizes by attracting dispersing individuals, thus better buffering the population against stochastic events (Pechmann and Wilbur 1994). In areas with low-quality breeding habitat (e.g. sites where predatory fish have invaded) or population sinks, conspecific cues could be used to

attract individuals to nearby, higher-quality sites. In addition to spatially shifting breeding distributions, calls may also be used to temporally shift a species breeding period. Indeed, spadefoot calls in our experiment appeared to both stimulate earlier breeding and extend the spadefoot breeding period. Influencing anuran spatial and temporal breeding dynamics in such a manner may ultimately increase reproductive output and probability of egg and tadpole survival, and thereby increase population size.

While playbacks may be a useful management tool for certain species, there are a number of potential issues that must be considered. Importantly, potential playback areas should be carefully vetted for quality so that individuals are not attracted to ecological traps (Virzi et al. 2012). Indeed, birds have been successfully attracted by conspecific playback to settle in areas of low-quality habitat (Betts et al. 2008). Playbacks may also attract non-target species, including undesirable competitors, predators, or parasites (Diego-Rasilla and Luengo 2004, Trillo et al. 2016). While we did not see any noticeable response by heterospecific anurans to playbacks in any of our experiments, heterospecific information use is generally common between species that share some ecologically similar parameter (Seppänen et al. 2007). Additionally, playbacks may attract individuals carrying diseases (e.g. chytrid or ranavirus), thereby further elevating disease risk and transmission at breeding areas (Raitanen et al. 2014). Social cues may also be ineffective if they are not within a species' perceptual range, thus managers must consider the distance between source habitats and playback ponds before implementation (Fletcher and Sieving 2010). Given all of these considerations, the use of social cues could be an important tool in establishing and augmenting anuran populations in an era with few proven management methods for amphibians (Trenham and Marsh 2002) and unprecedented amphibian declines (Wake and Vredenburg 2008).

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TABLES AND FIGURES

Table 4.1. Breeding characteristics of study species. Breeding habitat and period pertain to our particular study site and do not reflect the variability of each species experienced across wider geographic ranges.

Species	Breeding Habitat	Breeding	Study
		Period	Site
Cope's gray treefrog	Seasonal	Prolonged	IL, IN
Green frog	Permanent	Prolonged	IL
Wood frog	Seasonal	Explosive	IN
Spring peeper	Ephemeral-Permanent	Prolonged	IL
Mexican spadefoot	Ephemeral	Explosive	AZ
Arizona treefrog	Permanent	Explosive	AZ
American toad	Permanent	Explosive	IN

Table 4.2. Timing of playbacks for each species tested in Indiana, Illinois, and Arizona.

Site	Species	Playback Started	Playback Ended
IN	American toad	3/29/2014	4/24/2014
	Cope's gray treefrog	4/24/2014	7/14/2014
	Wood frog	3/12/2015	3/24/2014
IL	Cope's gray treefrog/Green frog	5/21/2014	7/25/2014
	Spring peeper	3/9/2015	4/13/2015
	Spring peeper/Cope's gray treefrog	4/13/2015	5/19/2015
	Cope's gray treefrog/Green frog	5/19/2015	7/24/2015
AZ	Mexican spadefoot	6/30/2016	8/8/2016
	Arizona treefrog	6/30/2016	8/8/2016

Table 4.3. Colonization rate of playback and control ponds with a Fisher’s Exact Test for significance, log rank test for difference in latency to first colonization between playback and control, and percentage of playback and control pools with adults observed.

Species	Site	Colonization Rate		Fisher's Exact Test	Latency to Colonization	Adults Observed	
		% Playback Ponds	% Control Pond			% Playback	% Control
Cope’s gray treefrog	IN	78 (7/9)	11 (1/9)	p = 0.015	p = 0.005	100 (9/9)	33 (3/9)
	IL ^a	22 (2/9)	22 (2/9)	p = 1.000		33 (3/9)	11 (1/9)
Green frog	IL ^a	0	0			0	0
Wood frog	IN	67 (6/9)	44 (4/9)	p = 0.637	p = 0.463	89 (8/9)	78 (7/9)
Spring peeper	IL	0	0			11 (1/9)	0
Mexican spadefoot	AZ	57 (4/7)	0	p = 0.069	p = 0.023	71 (5/7)	14 (1/7)
Arizona treefrog	AZ	13 (1/8)	0			0	0
American toad	IN	0	0			0	0

^a Applies only to 2015 experiment. For *H. chrysoscelis* in 2014, only 1 playback pond was colonized. For *L. clamitans* in 2014, no ponds were colonized.

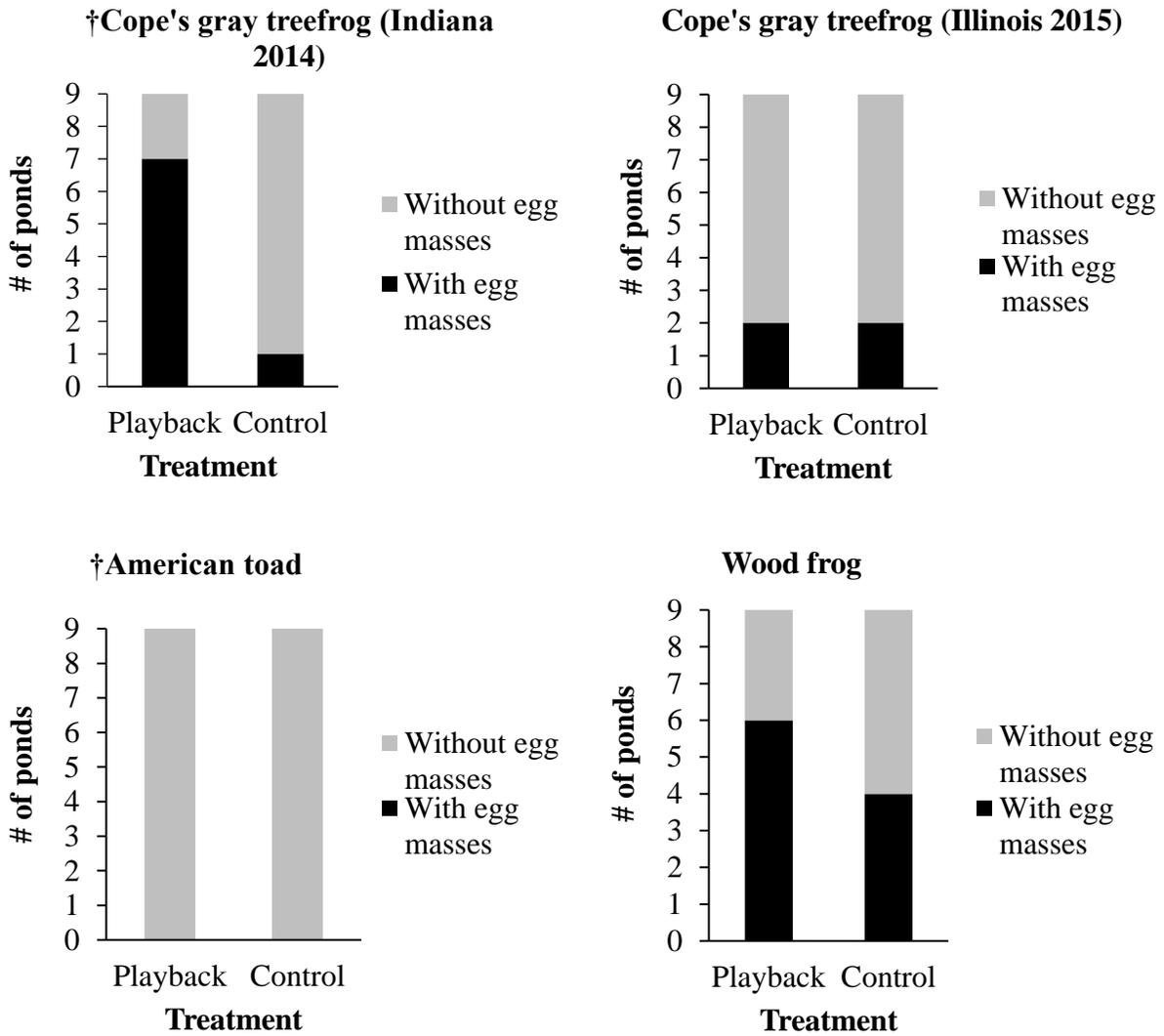


Figure 4.1. Number of playback and control ponds with egg masses detected for each specie.
 †Previously published in Buxton et al. (2015).

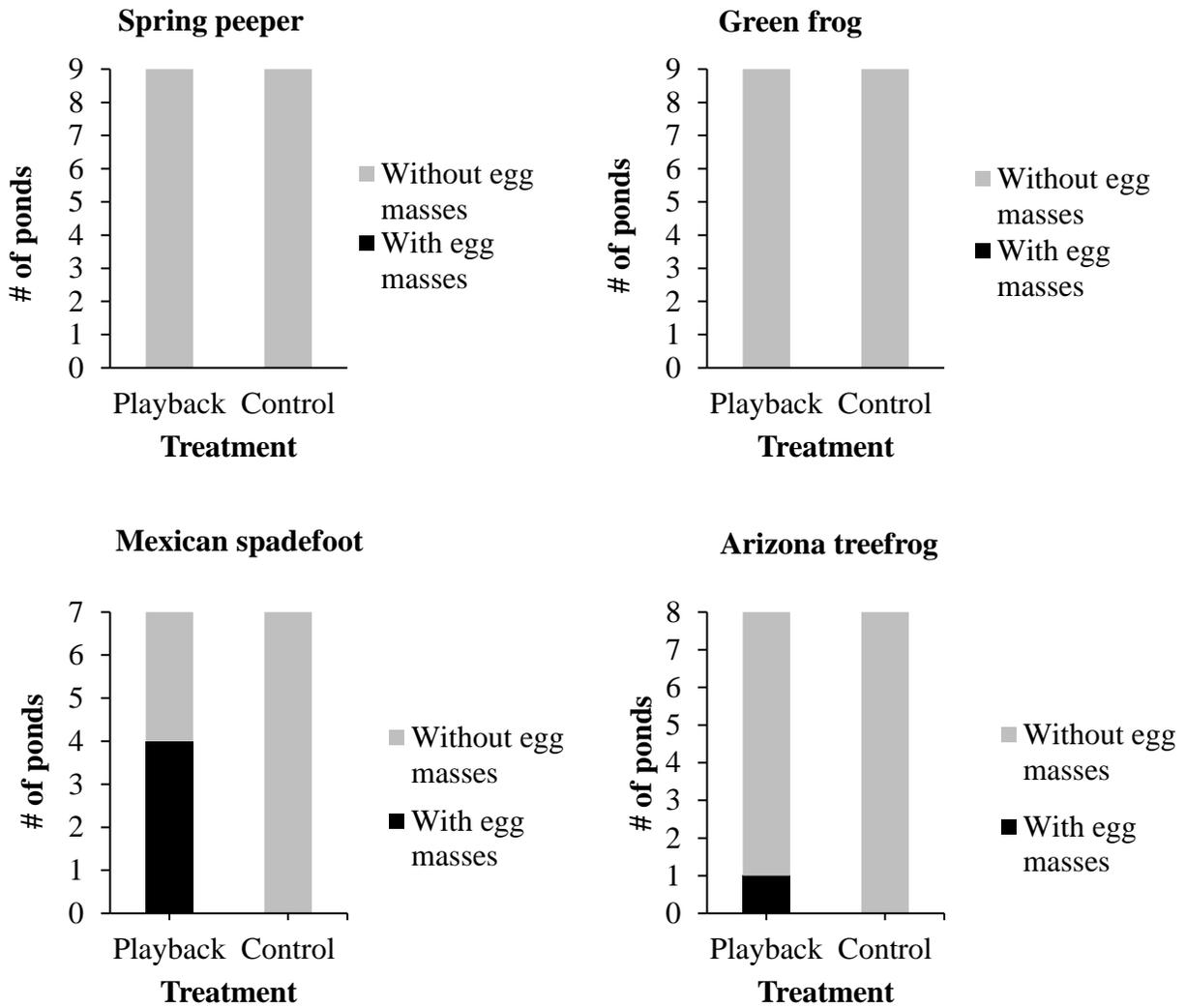
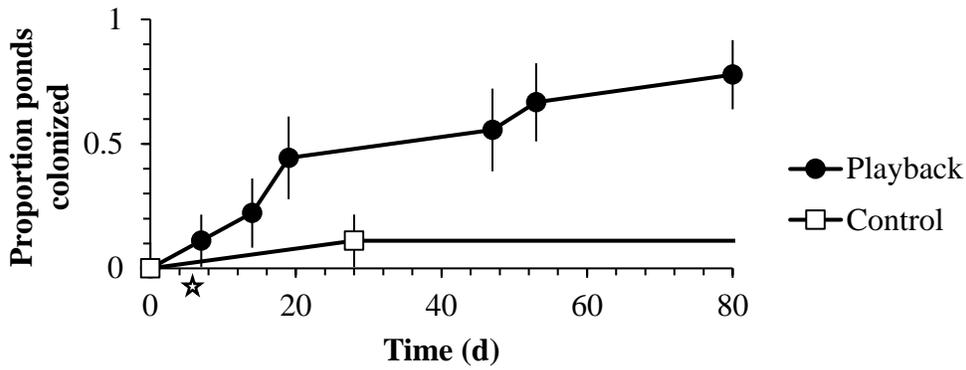
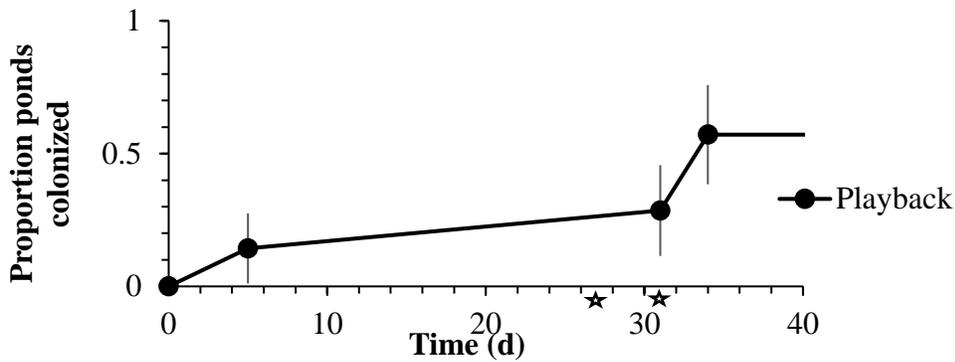


Figure 4.1 (cont.)

a) †



b)



c)

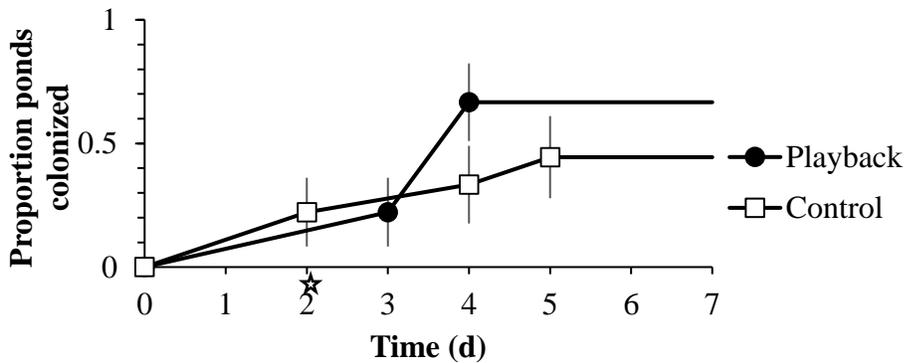


Figure 4.2. Colonization curves depicting time (in days) until first oviposition event of ponds by treatment for **a)** Cope's gray treefrog in Indiana, 2014; **b)** Mexican spadefoot in Arizona, 2016; **c)** Wood frog in Indiana, 2015. Stars on x-axis indicate when species was first heard calling in surrounding environment (stars for Mexican spadefoot indicate the two nights when species was primarily heard calling). † Previously published in Buxton et al. (2015).

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CHAPTER 5: FROG BREEDING POND SELECTION IN RESPONSE TO PREDATORS AND CONSPECIFIC CUES⁴

ABSTRACT

Predators are a major influence on the breeding site selection decisions of anurans. Many species actively avoid breeding in habitat with predators when given the choice between predator and predator-free sites. However, certain factors such as site fidelity or conflicting cues may preclude avoidance behavior. We conducted two experiments examining how western chorus frogs, *Pseudacris triseriata*, respond to predators, western mosquitofish, *Gambusia affinis*, using an array of artificial ponds located at two field sites. In one experiment, we added *G. affinis* to half of our experimental ponds and monitored subsequent colonization by frogs. We found that frogs laid significantly fewer eggs in ponds with fish compared to fishless ponds. In another experiment, we introduced an additional cue to complicate the decision making process and monitored colonization of ponds in response to treatments of conspecific breeding cues only (eggs), predators (*G. affinis*) only, and conspecific cues and predators. We found no significant differences in number of eggs deposited among these three treatments. Based on these results, *P. triseriata* does not always exhibit complete avoidance of fish predators, and avoidance may vary based on factors such as site fidelity or dispersal costs. This study represents a step towards understanding how multiple biotic factors at a breeding pond may influence site selection behavior of anurans in the field.

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INTRODUCTION

Predators often play a major role in shaping habitat selection decisions for breeding individuals (Resetarits 1996). Predators may not only cause direct mortality of breeding adults themselves, but may also pose a threat to the survival and growth of future offspring (Binckley & Resetarits 2002). Consequently, selecting appropriate habitat with few or no predators is crucial for many animals. Prior to selecting a breeding area, animals may evaluate the safety and quality of habitat through the presence of already established conspecifics (Ahlering et al. 2010), or through direct sampling of predators or predator cues (Mokany & Shine 2003). Indeed, many species assess risk of predation at several potential sites during the habitat selection process and choose the site with the lowest risk of predation (Cupp 1994, Emmering and Schmidt 2011, Wesner et al. 2012). For example, *Culex* mosquitoes preferentially oviposit in ponds without predator chemical cues (Angelon & Petranka 2002) and songbirds preferentially nest in areas with reduced predator communities (Fontaine & Martin 2006).

For those species with no parental care, the selection of a suitable, safe site for offspring growth and development is of particular importance (Crump 1974). Such is the case with many species of anuran amphibians that reproduce in a pond and depart immediately after oviposition (i.e. egg laying). While eggs of certain species may have chemical or mechanical defenses (e.g. unpalatability, protective jelly) to protect from predation, others are largely unprotected and vulnerable to a wide variety of predators (Grubb 1972). Similarly, while larvae of some species have specific mechanisms to successfully cope with predators (e.g. reduced mobility, unpalatability), others are relatively defenseless until they metamorphose and leave the pond (Kats et al. 1988). Thus, for some anuran species, appropriate habitat selection by adults may be the primary line of defense against offspring predation and, as such, the ability to detect and

avoid predators should be under strong selective pressure (Hecnar & M'Closkey 1997, Resetarits 1996).

Previous studies have experimentally demonstrated that when given a choice between pools with and without predators, adults of certain anuran species are indeed able to detect and avoid breeding in pools with predators (Binckley & Resetarits 2003, Brown et al. 2008, Vonesh et al. 2009, Kraus et al. 2011). In temperate North America, Cope's gray treefrog, *Hyla chrysoscelis* has frequently been the target of such studies, and is almost always found to oviposit primarily in ponds without predaceous fish (Resetarits 2005, Binckley & Resetarits 2008, Kraus & Vonesh 2010). The effects of predators on the habitat selection decisions of other temperate anurans is not as clearly understood, although many field-based observational studies have consistently documented negative associations between fish and certain species (e.g. *Pseudacris triseriata*, *Rana muscosa*, etc., see Buxton & Sperry 2017). However, it is not well established whether these negative associations are the result of predation on offspring or habitat selection by adults. Indeed, the ability to assess and select habitat based on predator presence may evolve only under certain conditions, such as when larvae are highly vulnerable to predators (i.e. suffer high mortality), when predators are patchily distributed throughout an area (i.e. sites with and without predators are available), when predators are sufficiently common, or when predators are relatively predictable in behavior (i.e. predators do not enter and leave areas randomly; Blaustein 1999).

Although anurans may be able to detect predators, certain circumstances may preclude or negate them from effectively avoiding these predators. For example, site fidelity to particular areas may result in individuals selectively returning to low-quality habitat (Matthews & Preisler 2010). For example, Matthews & Preisler (2010) found that Sierra Nevada yellow-legged frogs,

Rana Sierrae, showed high levels of site fidelity to previously used ponds despite the presence of introduced trout, suggesting that while site fidelity once may have been a beneficial strategy for these frogs, it may now be contributing to population declines. Alternatively (but not mutually exclusively), high movement or dispersal costs from low-quality breeding sites could reduce habitat selection and lead to increased use of poor sites (Sutherland 1996).

The presence of conspecific cues may also alter individual perception of predators and predation risk by indicating high quality or safe habitat. Indeed, individuals from a variety of taxa are attracted to and preferentially settle near conspecific cues, and use information from conspecifics to determine resource quality or predator presence (Stamps 1988, Templeton et al. 2005, Ahlering et al. 2010). Female mosquitoes, for example, preferentially oviposit in ponds containing conspecific larvae (Mokany and Shine 2003) and female keelback snakes, *Tropidonophis mairii*, selectively oviposit in sites containing empty conspecific eggshells (Brown & Shine 2005). However, if conspecific cues are present in low-quality areas, an ecological trap may arise where information from conspecifics is unreliable or misleading and results in decreased fitness (Giraldeau et al. 2002). For anuran amphibians, there has been little work investigating the nuances of conspecific cues on breeding habitat selection decisions (but see Marsh and Borrell 2001, Murphy 2003, Buxton et al. 2015) but ecological traps in other taxa have been found to arise based on conspecific cues. Such is the case for black-throated blue warblers, *Setophaga caerulescens* that have been induced by conspecific song to settle in areas of poor quality habitat (Betts et al. 2008) and nutmeg manikins, *Lonchura punctulata*, persuaded by videos of conspecifics to feed at slow-dispensing feeders (Rieucan & Giraldeau 2009).

We investigated how the presence of western mosquitofish predators, *Gambusia affinis*, influenced oviposition decisions of western chorus frogs, *Pseudacris triseriata*, in two separate

field experiments. *P. triseriata* is a small hyliid common throughout large parts of North America that breeds in a variety of water bodies but is most often found in areas lacking fish. Eggs are deposited in small masses attached to vegetation several centimeters below the surface of the water (Dodd 2013). Deposition occurs over an extended breeding period and egg hatching time can vary considerably depending on water temperature (in cold temperatures, hatching may take 15 to 27 days; Whitaker 1971). Resultant larvae lack effective defenses against predators (Kats et al. 1988). *G. affinis* is a small, live-bearing fish and known predator of amphibian eggs and larvae, and has been found to consume significant amounts of *P. triseriata* tadpoles (Zieber et al. 2008). In one experiment, we investigated response to *G. affinis* using an array of artificial ponds containing fish or no fish. In another experiment, we investigated response to both *G. affinis* and conspecific cues using an array of artificial ponds containing conspecific eggs only, predators only, or both conspecific eggs and predators. Because *P. triseriata* eggs and larvae are vulnerable to depredation by fish, we predict that frogs should exhibit avoidance of ponds containing *G. affinis* regardless of other factors such as prior history of site use or presence of conspecific cues.

METHODS

Predator experiment

To determine whether *P. triseriata* avoid ovipositing in ponds with *G. affinis* predators we conducted an experiment using an array of artificial ponds with and without fish. We conducted this experiment at Sparta Training Area in Sparta, IL during March-April 2016. In late May 2014, we had established 18 artificial garden ponds (1.7 m x 1.2 m, 344 L capacity) made of a flexible polyethylene pond liner in a grid throughout the study site as part of a larger ongoing study. Ponds were located 200 m apart from one another in an area composed primarily

of grassland interspersed with shrubs and constructed lakes. In 2014, five ponds were found to contain chorus frog egg masses and in 2015 all pools contained chorus frog egg masses. Because all pools had a history of colonization, we randomized fish predator treatment among the eight ponds in the northern section of the site and the ten ponds in the southern section (Fig. 5.1). We obtained *G. affinis* from a private pond in western Illinois and added five fish to each treatment pond on March 2, 2016. Fish were contained within fiberglass mesh enclosures that allowed the passage of visual and chemical cues. Enclosures consisted of window screen lining attached to a floating foam ring, with a wire structure for internal support. Mesh enclosures were also placed in control ponds, but did not contain any fish. We subsequently checked ponds every 2-3 days for egg masses and counted both number of masses and number of eggs. After counting, we removed eggs and placed them in a nearby body of water in order to eliminate any confounding cues that eggs might provide and to allow more accurate counts. We also anecdotally noted the number of chorus frogs in the pond and their activity (e.g. calling, amplexus, etc.). We terminated the experiment on April 8, 2016 when no egg masses had been detected at any ponds in over a week.

Predator/conspecific experiment

To explore the effects of *G. affinis* predators and conspecific cues on *P. triseriata* oviposition site selection, we conducted an experiment using an array of artificial ponds containing conspecific cues only, predators only, or both conspecific cues and predators. We conducted this experiment at Camp Atterbury Joint Manuever Training Center in Edinburgh, IN during March 2016. In March 2014, we had established 18 artificial breeding ponds with the same specifications as described previously. Ponds were located 140 m apart from one another in a forested area containing a constructed permanent pond and several seasonal ponds and

wetlands. In 2014, three ponds were colonized with *P. triseriata* egg masses and in 2015, seven additional ponds contained egg masses and tadpoles. Because we believed that colonization history could have some effect on oviposition site selection decisions, we randomized treatments among the ten ponds with a prior history of colonization and separately randomized treatments among the remaining eight ponds for a total of six ponds per treatment (Fig. 5.2). Using *G. affinis* from the same location as described above, we added five fish predators to the respective treatment ponds on March 4 and 5, 2016. For the conspecific cue, we gathered egg masses from earlier breeding events and placed the eggs in the respective treatment ponds concurrently with the predators. We note that if chemical cues are used to detect conspecific presence, then lingering cues from egg masses removed from ponds before the start of the predator/conspecific experiment (i.e. one pond already containing egg masses was subsequently assigned the treatment of predator only) could have potentially remained in ponds. However, we think it is unlikely because persistence of waterborne chemical cues appears to be relatively short-lived (Ferrari et al. 2008, Ferrari et al. 2010) and there were two days in between addition of treatments to ponds and the occurrence of natural breeding in those ponds. We used approximately 200 eggs for each treatment pond, which is on the low end of density of eggs laid in a natural breeding event. We placed eggs in the same location in each pond and marked each mass with visible implant elastomer so we would be able to distinguish masses from those laid later. We subsequently checked ponds every 1-2 days for egg masses and counted both number of masses and number of eggs. After counting, we removed eggs and placed them in a nearby body of water. As above, we anecdotally noted number and activity of chorus frogs upon approach to ponds. Ponds regularly received egg masses until March 16, 2016 at which point no

eggs were found in ponds for more than two weeks. Thus, we considered March 16 the last day of the experiment.

Data analysis

We compared differences in number of eggs and egg masses between treatment and control ponds for the predator experiment using unpaired two-sample t-tests after confirming assumptions of normality and homogenous variances. Additionally, we considered that the spatial distribution of our ponds could have potentially influenced egg distribution if the two ponds in the middle of the matrix, both of which were predator ponds, were less likely to be colonized regardless of treatment. To account for this, we assigned an egg count total to each of the center predator ponds equivalent to the average egg count for control ponds and re-ran the analysis. For the predator-conspecific experiment, we compared differences in number of eggs and egg masses using Kruskal-Wallis tests for non-parametric data after confirming that the data did meet the assumption of homogenous variances but were not normally distributed. For both experiments, we conducted a survival analysis examining time to first colonization event and used a log-rank test to determine whether latency to first colonization significantly differed between treatment and control ponds.

RESULTS

Predator experiment

P. triseriata deposited eggs and egg masses in nearly every pond regardless of predator presence (8 of 9 predator ponds and 9 of 9 control ponds with eggs). However, the amount of eggs and egg masses was significantly different between treatment and control (eggs: $t_{16} = -4.602$, $p = 0.0001$; egg masses: $t_{16} = -4.563$, $p = 0.0002$). At predator ponds, we documented a total of 12,645 eggs and 239 egg masses, resulting in an average of 1,405 eggs and 26.56 egg

masses per pond (SE: 420.15 eggs; SE: 7.57 egg masses). At control ponds, we documented a total of 46,202 eggs and 854 egg masses, resulting in an average of 5,133 eggs and 94 egg masses per pond (SE: 692.78 eggs; SE: 12.92 egg masses; Fig. 5.3a). Control ponds were more likely to be colonized before predator ponds ($\chi^2 = 6.4$, $df = 1$, $p = 0.0113$; Fig. 5.3b).

Additionally, we did not find any evidence that the spatial distribution of treatment influenced results; a significant avoidance of predators was still apparent even when assigning egg count totals to the two center predator ponds equivalent to the average received by control ponds ($t_{16} = -2.881$, $p = 0.0109$). We anecdotally documented a total of 14 adult frog sightings in predator ponds, resulting in an average of 1.6 frogs per pond over the course of the experiment and 39 adult frog sightings in control ponds, resulting in an average of 4.3 frogs per pond. We note that it is likely individuals remained in the pond over the course of multiple days, thus they were likely double counted in these totals.

Predator/conspecific Experiment

All ponds found with *P. triseriata* egg masses in previous years again contained chorus frog egg masses during the course of this study, regardless of fish presence. No colonization of new ponds occurred. Of the 10 ponds in which eggs were laid, 4 were predator only ponds, 3 were predator/conspecific ponds, and 3 were conspecific only ponds. Unlike the predator experiment, however, there were no significant differences in number of eggs or egg masses among treatments (egg masses and eggs: $H(2) = 0.04162$, $p = 0.979$). At predator ponds, we documented a total of 5,740 eggs and 177 egg masses, resulting in an average of 956.67 eggs and 29.50 egg masses per pond (SE: 453.10 eggs; SE: 15.50 egg masses). At predator/conspecific ponds, we documented a total of 7,985 eggs and 219 egg masses, resulting in an average of 1330.83 eggs and 36.50 egg masses per pond (SE: 872.74 eggs; SE: 23.70 egg masses). At

conspecific only ponds, we documented a total of 6,000 eggs and 187 egg masses, resulting in an average of 1,000 eggs and 31.17 egg masses per pond (SE: 545.22 eggs; SE: 17.68 egg masses; Fig. 5.4a). There was no difference in time to first colonization event among treatments ($\chi^2 = 0.4$, $df = 2$, $p = 0.806$; Fig. 5.4b) We anecdotally documented a total of 18 frog sightings in predator only ponds, resulting in an average of 3 frogs per pond; 32 total frogs in predator/conspecific ponds, resulting in an average of 5.3 frogs per pond; and 34 frogs in conspecific only ponds, resulting in a total of 5.7 frogs per pond.

DISCUSSION

We found that the majority of breeding in our predator experiment occurred in fishless ponds, suggesting that behavioral avoidance is at least partially responsible for associations between *P. triseriata* and its predators. However, we also found that avoidance was not universal and that behavioral decisions can be site and context dependent. In our predator only experiment, we found that the average number of eggs and adults were lower at predator ponds compared to control ponds. Additionally, colonization of predator ponds occurred later than controls, potentially indicating that once saturation occurs at high-quality sites, adults spill-over into less desirable sites (Fretwell and Lucas 1970). These results are not particularly surprising given the many studies that have documented avoidance of fish by *H. chrysoscelis*, a closely related species with a similar breeding ecology and susceptibility to fish predation (e.g. Binckley & Resetarits 2008, Vonesh et al. 2009).

We did not observe an avoidance of fish in our predator/conspecific experiment. There are a number of non-mutually exclusive explanations for this finding, including site or population differences between the two experiments or an artifact of the experimental design itself. In general, reproductive effort was much lower in the predator/conspecific experiment but

average egg counts for each treatment in the predator/conspecific experiment were similar to the average egg count for the predator treatment in the predator only experiment. In the predator/conspecific experiment, adults may have viewed all of the treatments as “bad choices” or poor-quality habitat and reduced reproductive effort in ponds or reproduced elsewhere. Anecdotally, we note that ponds found with egg masses were often in close proximity to a potential breeding area (i.e. a small ephemeral pool, tire rut, or seasonal pond), making it possible that saturation at these sites resulted in individuals moving to our ponds. Previous studies have similarly documented a switch by *H. chrysoscelis* to sites with fish when fishless sites become saturated by conspecifics (Rieger et al. 2004, Binckley and Resetarits 2008). Thus, if *P. triseriata* did avoid all ponds equally, this would result in the appearance of non-avoidance of predators.

While not directly lethal, like predators, conspecific larvae can negatively affect survival and development of other individuals and may also be avoided by ovipositing adults. Indeed, results from experimental studies generally show that adults selecting breeding habitat in arrays of artificial ponds tend to avoid pools with conspecific larvae (Resetarits & Wilbur 1989, Murphy 2003, Glos et al. 2008). While we expected that in a more variable environment conspecifics might act as a positive cue of habitat quality (Rudolf and Rödel 2005), our results indicate that this may not necessarily be the case. Results from other studies on this topic are mixed; Marsh and Borrell (2001) found that egg masses were not used as a cue for oviposition by Túngara frogs, *Engystomops pustulosus*, in natural stream pools while Rudolf and Rödel (2005) found that breeding Guinea river frogs, *Phrynobatrachus guineensis*, were attracted to the presence of conspecific eggs and larvae, presumably because they signaled site quality and lack of predators.

Differential movement costs (potentially in conjunction with only poor habitat choices) at the predator/conspecific experiment site may also have resulted in reduced habitat selection and consequently lessened predator avoidance. Theory predicts that if search costs are high, individuals are more likely to remain in areas of low-quality habitat (Sutherland 1996). If dispersal costs (e.g. risk of predation, desiccation) were particularly high at the predator/conspecific site compared to the predator only experiment site, individuals may have been more likely to breed in the pond they first encountered rather than search for a better location. Compared to many previous studies, our study used ponds located hundreds of meters apart rather than ponds located only tens of meters apart (e.g. Resetarits & Wilbur 1989, Binckley & Resetarits 2002, Rieger et al. 2004), making it unlikely that individuals could readily move among and sample multiple sites. Correspondingly, Marsh et al. (2001) found that *Engystomops pustulosus* were more faithful to a particular pond if alternative ponds were located ≥ 10 m away. Clustering of treatments as a result of our randomization process may have also made certain treatments more difficult for frogs to travel to or locate. For example, if the four of the six conspecific only treatments located in the northern section of the site were more difficult to reach, then colonization may have been reduced at these sites and resulted in similar egg numbers between this treatment and other treatments then there may otherwise have been if treatments were more evenly distributed across the landscape.

Anurans can be highly site faithful (Pechmann et al. 2001, Piper 2011) and differences in philopatry between our sites could have influenced adult behavior. A particularly strong tendency to return to natal ponds at the site of the predator/conspecific experiment (potentially related to higher dispersal or movement costs) could have overrode any cues of habitat quality. This phenomenon has been observed in both frogs and birds, where individuals continue to

return to areas of low reproductive success or degraded habitat (Searcy 1979, Ganter & Cooke 1998, Linkhart and Reynolds 2007, Matthews & Preisler 2010). We did find that only ponds colonized in the previous year were colonized during our experiment but, because we did not mark frogs, we do not know whether individuals did indeed return to their natal ponds. However, some studies have anecdotally observed that *P. triseriata* does not move far from breeding sites during the non-breeding season, indicating that dispersal could be limited (Kramer 1973, Cochran 1989).

It is also possible that the lack of avoidance to fish displayed in our predator/conspecific study may be a logistical issue related to the type or number of fish used in the experiment. Although *G. affinis* are native to the region and have been recorded at the study site, we did not document any of these fish in the immediate vicinity of our experiment. However, *G. affinis* should have a shared evolutionary history with *P. triseriata*, resulting in an innate predator recognition (Carthey and Banks 2014). Alternatively, the number of fish at each pond (5) may have been insufficient to elicit a response. However, even low densities of predaceous fish can significantly impact larval abundance, particularly in a small, enclosed area with few refuges available such as in our ponds. Furthermore, previous studies have documented avoidance of fish even at very low densities (*Hyla femoralis* avoided a single 2-g fish; Rieger et al. 2004). Thus, we feel that both of these explanations are likely inadequate.

Finally, we note that male chorusing also likely plays an important role in female habitat selection and resultant oviposition dynamics. We observed male *P. triseriata* calling from predator ponds in both experiments, albeit in lesser numbers than at controls or other treatments. Why some males called at predator ponds despite the fitness consequences for offspring is unclear, but could be attributable to factors such as saturation by conspecific males at higher-

quality ponds or less investment in a single reproductive event as compared to females (Murphy 2003). Regardless, male calling at ponds may have stimulated some females to breed irrespective of pond quality. The potential ability of male calling to override other important cues in habitat selection has been little explored, although Cayuela et al. (2017) found attractive male calls were not able to supersede poor habitat quality for ovipositing female yellow-bellied toads (*Bombina variegata*).

Collectively, this study represents another step towards examining how multiple cues are used by anurans in the field when selecting breeding habitat. Compared to many previous studies, this study was likely more representative of the conditions anurans encounter in nature, where breeding ponds may be separated by large distances, site fidelity to particular ponds may be common, and multiple cues at a site may be present. Future work that can disentangle habitat selection from site fidelity while still replicating natural conditions (in terms of spatial structure and multiple cues), may allow us to better understand how frogs are making decisions in the environment.

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FIGURES

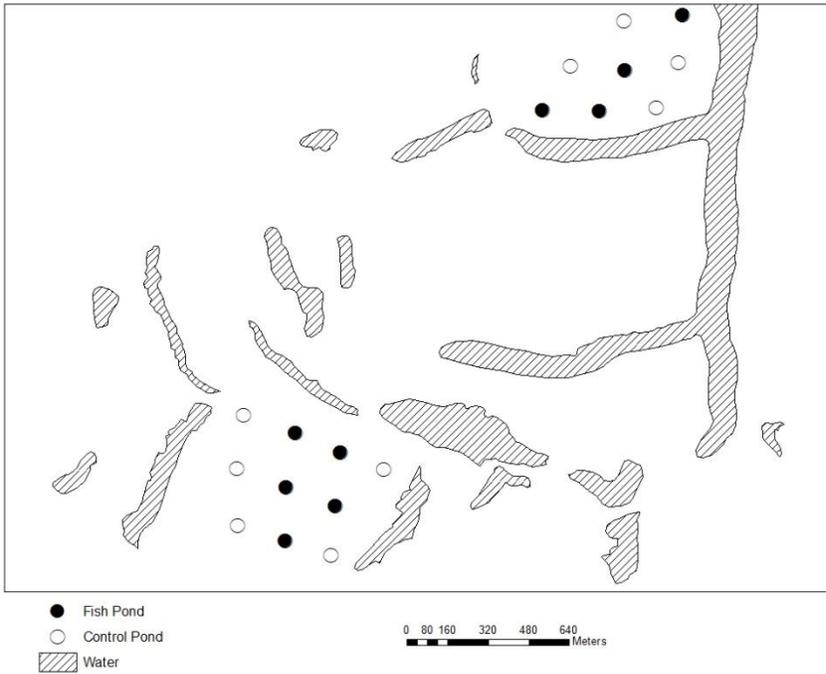


Fig 5.1. Schematic of experimental design at Sparta Training Area, Illinois in 2016. We randomly assigned half of the ponds as a predator treatment (*Gambusia affinis*) and the other half as controls and subsequently documented oviposition by *Pseudacris triseriata*.

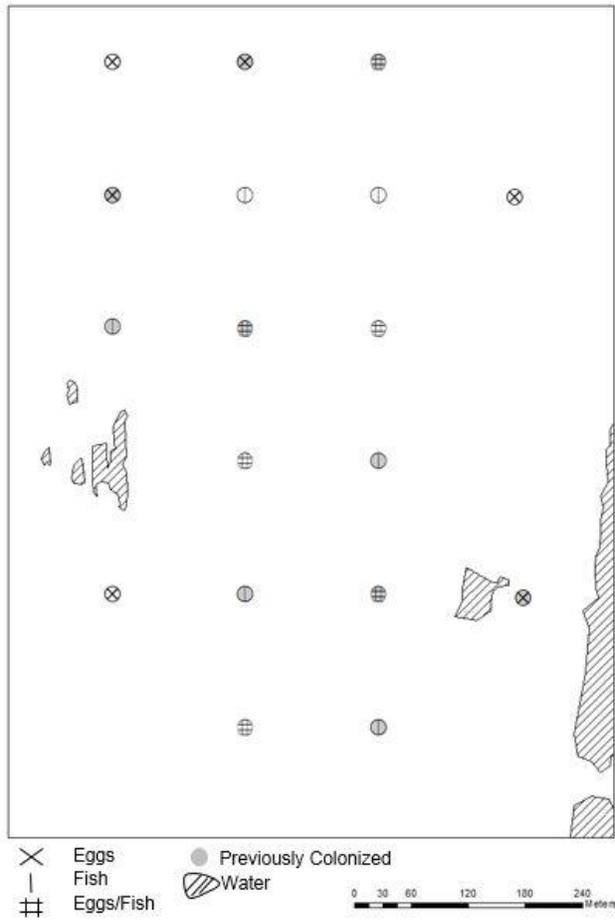


Fig 5.2. Schematic of experimental design at Camp Atterbury, Indiana in 2016. We randomly assigned treatment based on previous history of colonization (ponds that contained *P. triseriata* egg masses in previous years are indicated in gray). Treatments consisted of conspecific only (eggs), predator only (*Gambusia affinis*), and predator/conspicific. We subsequently documented oviposition by *Psuedacris triseriata*.

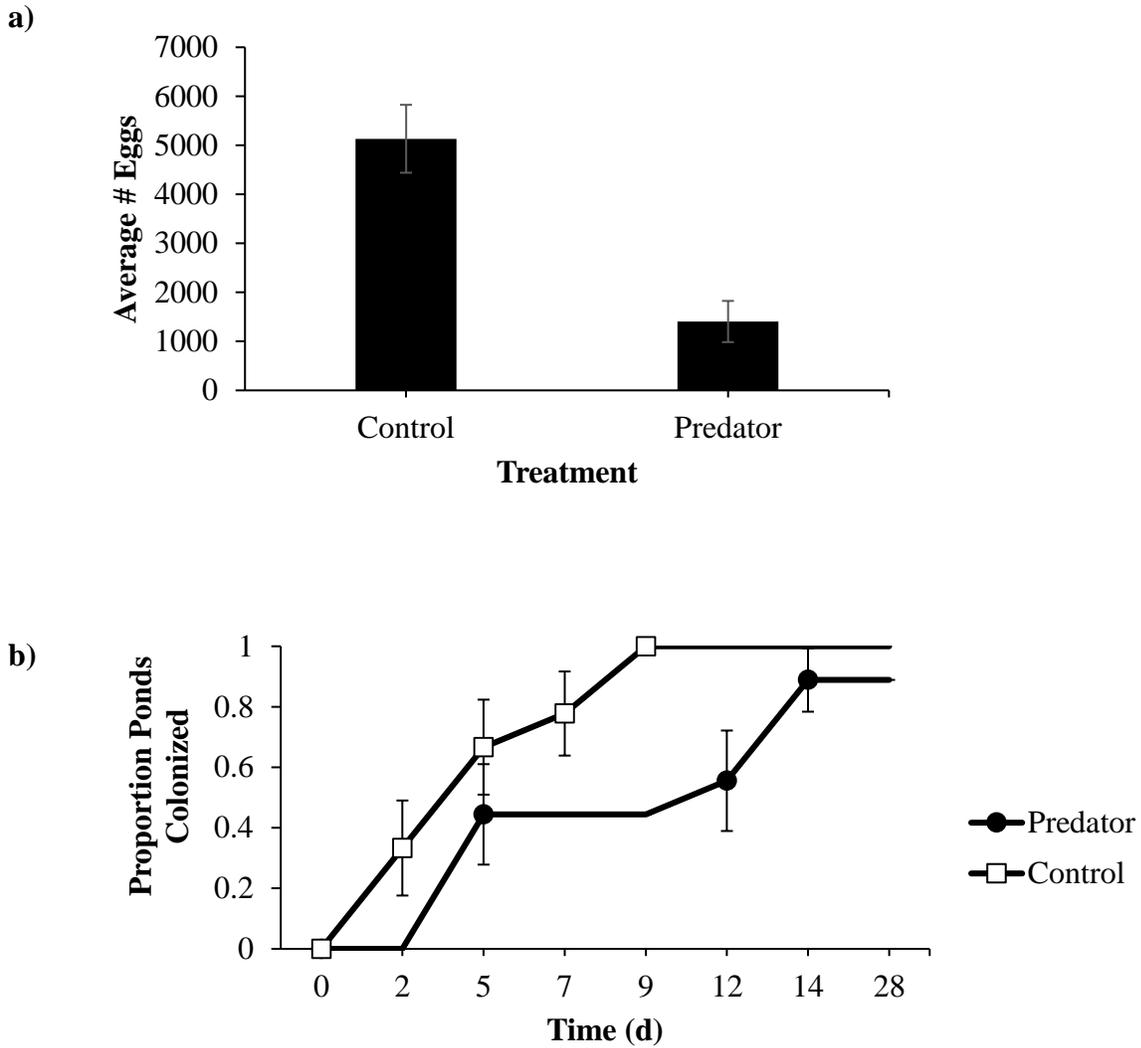


Fig 5.3. Graphs depict **a)** the average number of *Pseudacris triseriata* eggs found in each treatment for the predator/no predator experiment conducted at Sparta Training Area, IL and **b)** the time in days until first colonization (i.e. oviposition) event of ponds as represented by survival curves with associated standard error bars.

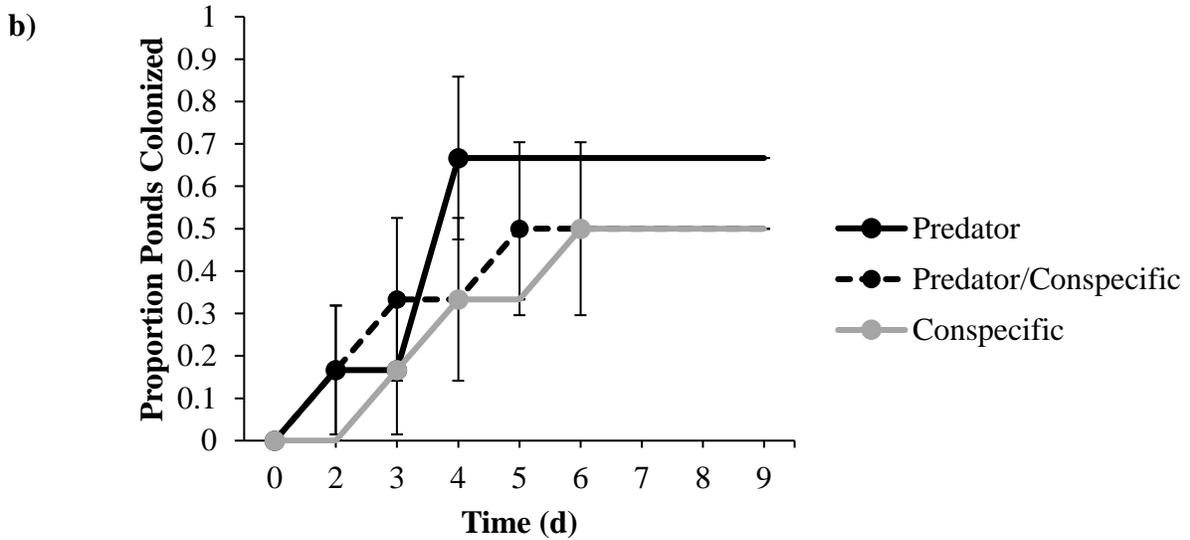
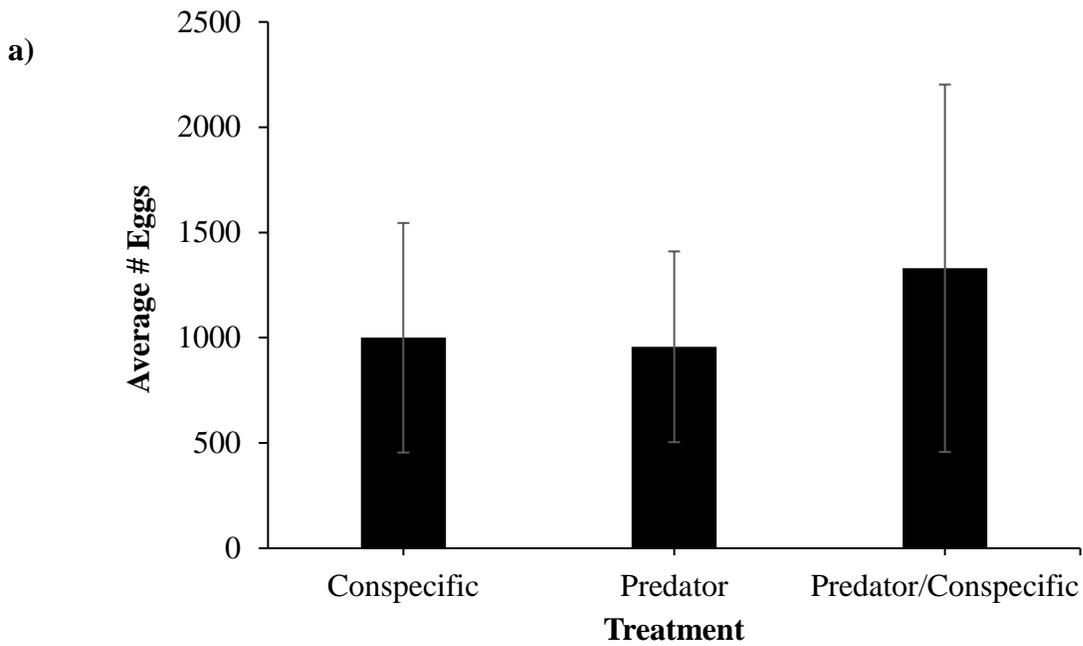


Fig 5.4. Graphs depict the **a)** average number of eggs found in each treatment for the predator/conspecific experiment conducted at Camp Atterbury, IN and **b)** the time in days until first colonization (i.e. oviposition) event of ponds as represented by survival curves with associated standard error.

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CHAPTER 6: SUMMARY

The general goal of my dissertation was to determine how information from conspecifics and predators influences location and selection of habitat by breeding anurans. In Chapter 2, I conducted a literature review of 43 recent studies examining the effects of conspecifics and heterospecifics (including predators) on anuran reproductive decisions. I found that in 75% of experimental tests, anurans avoided ovipositing in pools with conspecifics or heterospecifics (non-predatory). However, aggregation was documented as often as avoidance in field-based, observational studies. Aggregation could suggest conspecific attraction, or could simply be a reflection of preference for the same habitat. In 78% of experimental tests, anurans avoided ovipositing in pools with non-anuran predators. When considering predatory anurans, 72% of adults avoided depositing eggs or tadpoles in areas containing these predators. Collectively, results from a large number of studies indicate that anurans largely avoid predators. However, far fewer studies have directly examined conspecific influence, particularly in more realistic field settings.

While it has previously been suggested that anurans use conspecific chorus sounds to locate ponds, little field evidence for this existed. In Chapter 3, I examined whether two species of anurans, Cope's gray treefrogs (*Hyla chrysoscelis*) and American toads (*Anaxyrus americanus*), use conspecific chorus sounds to find breeding ponds. I suspected that differences in the breeding ecologies of each species might contribute to differences in strength of response. To test responsiveness, I broadcast chorus sounds at a subset of experimental ponds and designated the remaining ponds as silent controls. Over the course of the experiment, I found that 78% of playback ponds contained treefrog eggs while only 11% of control ponds contained eggs. Latency analysis indicated that playback ponds were colonized faster than the control pond.

Additionally, opportunistic visual and auditory surveys revealed 100% of playback ponds and only 33% of control ponds with treefrog adults. I found no American toad egg masses in any of the experimental ponds and observed no adults using the ponds during the course of the experiment. I considered that use of conspecific calls to locate new breeding ponds may be of little benefit for this population of toads that already had prior knowledge of a large, stable water source and only a limited time in which to breed. Conversely, I suggested that the prolonged breeding season of treefrogs combined with their tendency to breed in more seasonal ponds contributed to their responsiveness.

Based on the results of Chapter 3, it appeared that breeding ecology could potentially influence social information use in anurans. Thus in Chapter 4 I further investigated responsiveness to conspecific chorus sounds among five additional species across three field sites using the same methods as described above. I found a strong response by Mexican spadefoots (*Spea multiplicata*), but observed weak or no response by Arizona treefrogs (*Hyla wrightorum*), green frogs (*Lithobates clamitans*), Cope's gray treefrogs in Illinois, wood frogs (*Lithobates sylvaticus*), and spring peepers (*Pseudacris crucifer*). When considering both these results and the results from Chapter 3, few consistent patterns emerged regarding influence of breeding characteristics on responsiveness to chorus sounds. However, both species with a strong response to calls (Cope's gray treefrogs and Mexican spadefoots) tended to breed in more seasonal or temporary pools. Interestingly, both of these species encompassed the continuum of temporal patterns in anuran reproduction, with treefrogs as a prolonged breeder and spadefoots as an explosive breeder. Collectively, these results indicate that anuran use of conspecific calls is likely context-dependent, and that multiple factors (e.g. breeding duration, breeding habitat use,

species physiological characteristics, habitat and landscape characteristics) influence these circumstances.

After arriving at a pond, additional factors such as predators and conspecific cues (i.e. presence of egg masses or tadpoles) may influence whether anurans decide to use the pond for breeding. Generally, anurans avoid breeding in ponds with predators and competitors. However, avoidance behavior may vary if there is a prior colonization history of the pond, large distances between breeding ponds, or if conspecific cues act as a signal of habitat quality. In Chapter 5, I explored the relationship between anuran oviposition decisions and the presence of predators and conspecifics by adding predators and conspecific cues to experimental ponds. In an experiment conducted in southern Illinois using predators only, we found that western chorus frogs (*Pseudacris triseriata*) oviposited fewer eggs in ponds containing mosquitofish predators (*Gambusia affinis*) and colonized predator ponds significantly later than ponds without predators. In an experiment conducted in central Indiana using treatments of predators, conspecific cues, and predators combined with conspecific cues, we found no significant differences in number of eggs oviposited in each treatment. Latency analysis also indicated no differences in temporal patterns of colonization of each treatment. The reason for these differences in reproductive decisions between experiments is unclear, but higher site fidelity to ponds, higher dispersal or search costs, or across-the-board low habitat quality among all ponds at the Indiana field site may have contributed to the predator non-avoidance behavior.

Researchers have long sought to understand how various biotic and abiotic factors influence breeding decisions in anurans. My research has provided insight into how social information can influence location and selection of breeding habitat by anurans. Additionally, I have shown that social information use is not uniform across all species or populations. Future

research should continue to investigate how social information use differs according to life history characteristics, breeding ecology, age, and even personality. Further research is also needed to elucidate the more nuanced cues anurans might use in selection of breeding habitat.

APPENDIX A: CORRELATORY RELATIONSHIPS BETWEEN ANURANS AND FISH PREDATORS⁵

Summary of correlational field studies examining associations between fish and anuran presence (P) or abundance (N) during egg stage (E), tadpole stage (T), metamorph stage (M), juvenile stage (J), adult stage (A), or a combination of all stages (C). Positive associations with fish is indicated by +, negative associations by –, and no association with 0. Reference includes location of study and status of fish (i.e. introduced fish, native fish, combination of introduced and native, or not specified in the paper).

Species	Stage	Response variable	Association	Reference (including location and status of fish examined)	Potential mechanisms proposed by authors
Family Alytidae					
<i>Alytes obstetricans</i>	C	P, N	0	Orizaola and Braña 2006 (northern Spain: introduced)	Larvae hatch at advanced stage and large size, vegetation provides refuge
Family Bufonidae					
<i>Anaxyrus americanus</i>	E	N	–	Holomuzki 1995 (westcentral Kentucky, U.S.: not specified)	Adult avoidance of ponds with fish, larvae reduce activity and aggregate in groups
	T	P	+	Shulse et al. 2010 (northern Missouri, U.S.: native)	Unpalatable larvae

⁵ This material has been published in *BioScience*. Full citation: Buxton, V. L., and J. H. Sperry. 2017. Reproductive decisions in anurans: A review of how predation and competition affects the deposition of eggs and tadpoles. *BioScience* 67:27-38

Appendix A (cont.)

	C	P	0	Hecnar and M'Closkey 1997 (southwestern Ontario, C.A.: not specified); Porej and Hetherington 2005 (central Ohio, U.S.: not specified); Petranka et al. 2007 (western North Carolina, U.S.: not specified)	Hecnar and M'Closkey 1997, Porej and Hetherington 2005: Unpalatable larvae
<i>Anaxyrus canorus</i>	C	P	0	Knapp 2005 (eastcentral, California, U.S.: introduced)	Unpalatable larvae
<i>Anaxyrus boreas</i>	T	P	+	Hirner and Cox 2007 (southcentral British Columbia, C.A.: introduced)	Vegetation provides refuge, unpalatable larvae, fish reduce invertebrate predators
	C	P	+	Welsh et al. 2006 (northern California, U.S.: introduced)	Unpalatable larvae, fish reduce invertebrate predators
<i>Bufo bufo</i>	T	P, N	0	van Buskirk 2005 (north-central Switzerland: not specified)	Unpalatable larvae
	A	N	+	Martínez-Solano et al. 2003 (northcentral Spain: introduced)	Require similar habitat to fish, coexist with native fish
	C	P	0	Orizaola and Braña 2006 (northern Spain: introduced); Hartel et al. 2007 (central Romania: combination)	Orizaola and Braña 2006, Hartel et al. 2007: Unpalatable larvae and adults

<i>Bufo b. spinosus</i>	E, T	P	+	Indermaur et al. 2010 (northeastern Italy: not specified)	
<i>Bufo viridis</i>	E, T	P	+	Indermaur et al. 2010 (northeastern Italy: not specified)	
<i>Epidalea calamita</i>	A	N	-	Martínez-Solano et al. 2003 (northcentral Spain: introduced)	
<i>Nannophryne variegata</i>	T	P, N	-	van Buskirk 2005 (northcentral Switzerland: not specified)	van Buskirk 2005: Palatable larvae
	C	P	0	Hartel et al. 2007 (central Romania: combination)	
Family Hylidae					
<i>Hyla arborea</i>	T	P, N	-	van Buskirk 2005 (northcentral Switzerland: not specified)	Palatable larvae
	A	N	-	Martínez-Solano et al. 2003 (northcentral Spain: introduced)	No historical exposure to fish
	C	P	-	Hartel et al. 2007 (central Romania: combination)	
<i>Hyla chrysoscelis</i>	C	P	-	Petranka et al. 2007 (western North Carolina, U.S.: not specified)	Adult avoidance of ponds with fish, larvae lack effective defenses
<i>Hyla intermedia</i>	C	P	-	Ficetola and Bernardi 2004 (northern Italy: not specified)	
<i>Hyla versicolor</i>	C	P	-	Hecnar and M'Closkey 1997 (southwestern Ontario, C.A.: not specified)	Palatable larvae
<i>Hyla versicolor/chrysoscelis</i> complex	T	N	-	Shulse et al. 2013 (northeast Missouri, U.S.: introduced)	Adult avoidance of ponds with fish

Appendix A (cont.)

<i>Litoria spp.</i>	T	P, N	-	Hamer and Parris 2013 (southeastern Australia: introduced)	Larvae are active swimmers and foragers, thus suffer higher rates of predation
<i>Pseudacris crucifer</i>	C	P	0	Petranka et al. 2007 (western North Carolina, U.S.: not specified)	
	C	P	-	Hecnar and M'Closkey 1997 (southwestern Ontario, C.A.: not specified); Porej and Hetherington 2005 (central Ohio, U.S.: not specified)	Hecnar and M'Closkey 1997: Palatable larvae, larvae do not increase refuge use in presence of fish
<i>Pseudacris maculata</i>	T	P	-	Amburgey et al. 2014 (northcentral Colorado, U.S.: combination)	Larvae may be palatable
	T	N	-	Shulse et al. 2013 (northeast Missouri, U.S.: introduced) ^a	Adult avoidance of ponds with fish
<i>Pseudacris regilla</i>	T	P	0	Hirner and Cox 2007 (southcentral British Columbia, C.A.: introduced)	Small effect of trout or low statistical power
	T	N	-	Reid 2005 (southwestern Oregon & northwestern California, U.S.: introduced)	Predation by fish, treefrogs may not be able to detect introduced fish chemical cues

Appendix A (cont.)

	C	P	-	Matthews et al. 2001 (eastcentral California, U.S.: introduced); Knapp 2005 (eastcentral, California, C.A.: introduced); Pearl et al. 2005 (western Oregon, U.S.: introduced); Welsh et al. 2006 (northern California, U.S.: introduced)	Pearl et al. 2005: Adaptation for rapid development over predator-avoidance traits (e.g. detection of chemical cues); Welsh et al. 2006: Palatable larvae
	C	N	-	Matthews et al. 2001 (eastcentral California, U.S.: introduced)	
<i>Pseudacris triseriata</i>	C	P	-	Hecnar and M'Closkey 1997 (southwestern Ontario, C. A.: not specified); Porej and Hetherington 2005 (central Ohio, U.S.: not specified)	Hecnar and M'Closkey 1997: Palatable larvae, larvae do not increase refuge use in presence of fish
Family Ranidae					
<i>Lithobates catesbeianus</i>	T	N	+	Werner and McPeck 1994 (southwestern Michigan, U.S.: not specified)	Unpalatable larvae, fish reduce invertebrate predators
	C	P	0	Hecnar and M'Closkey 1997 (southwestern Ontario, C.A.: not specified); Petranka et al. 2007 (western North Carolina, U.S.: not specified)	Hecnar and M'Closkey 1997: Large clutch size, large-bodied larvae and adults, unpalatable larvae, require same habitat as fish
	C	P	+	Porej and Hetherington 2005 (central Ohio, U.S.: not specified)	Porej and Hetherington 2005: Large clutch sizes, unpalatable larvae

Appendix A (cont.)

<i>Lithobates clamitans</i>	T	N	0	Shulse et al. 2013 (north-east Missouri, U.S.: introduced)	Larvae able to persist with fish
	T	N	-	Werner and McPeck 1994 (southwestern Michigan, U.S.: native)	Predation on larvae, larvae use microhabitat that exposes them to fish
	C	P	+	Hecnar and M'Closkey 1997 (southwestern Ontario, C.A.: not specified)	Large clutch size, large-bodied larvae and adults, unpalatable larvae, require same habitat as fish
	C	P	0	Porej and Hetherington 2005 (central Ohio, U.S.: not specified); Petranka et al. 2007 (western North Carolina, U.S.: not specified)	Porej and Hetherington (2005): Large clutch sizes, unpalatable larvae
<i>Lithobates palustris</i>	E	N	-	Holomuzki 1995 (west-central Kentucky, U.S.: not specified)	Adult avoidance of ponds with fish, larvae reduce activity, aggregate in groups
	C	P	0	Hecnar and M'Closkey 1997 (southwestern Ontario, C.A.: not specified)	Adults have toxic skin secretions
<i>Lithobates pipiens</i>	C	P	-	Hecnar and M'Closkey 1997 (southwestern Ontario, C.A.: not specified)	Palatable larvae, adults may detect predatory fish
<i>Lithobates sylvaticus</i>	E	N	-	Petranka and Holbrook 2006 (western North Carolina, U.S.: not specified)	Adult avoidance of ponds with fish
	M	N	-	Eaton et al. 2005 (northern Alberta, C.A.: native)	Predation on larvae

Appendix A (cont.)

	A	N	0	Eaton et al. 2005 (northern Alberta, C.A.: native)	Philopatric adults, adults have little time to sample ponds for fish before breeding occurs
	M, A	N	0	Schank et al. 2011 (southwestern Alberta, C.A.: introduced)	Regular co-occurrence with native fish thus frogs are not naïve to fish predators, lake productivity shortens larval development time and increases availability of alternative prey
	C	P	-	Petranka et al. 2007 (western North Carolina, U.S.: not specified)	Adult avoidance of ponds with fish, larvae lack effective defenses
	C	P	0	Hecnar and M'Closkey 1997 (southwestern Ontario, C.A.: not specified)	Palatable larvae
<i>Rana aurora</i>	T	P	0	Adams et al. 2011 (western Oregon, U.S.: introduced)	Wetland vegetation more important than fish
	T	A	0	Adams 1999 (western Washington, U.S.: introduced)	
	C	P	-	Pearl et al. 2005 (western Oregon, U.S.: introduced)	
<i>Rana cascadae</i>	T, J, A	P	-	Welsh et al. 2006 (northern California, U.S.: introduced)	Adults detect and avoid waters with fish, palatable larvae
	T, J, A	N	-	Pope 2008 ^b (northern California, U.S.: introduced)	Predation on larval and juvenile stages.

Appendix A (cont.)

<i>Rana dalmatina</i>	C	P	0	Hartel et al. 2007 (central Romania: combination)	
<i>Rana esculenta</i>	C	P	0	Ficetola and Bernardi 2004 (northern Italy: not specified); Hartel et al. 2007 (central Romania: combination)	
<i>Rana latastei</i>	E, T	P	+	Indermaur et al. 2010 (northeastern Italy: not specified)	
	C	P	0	Ficetola and Bernardi 2004 (northern Italy: not specified)	
<i>Rana luteiventris</i>	E, T	P	0	Pillioid et al. 2010 (northern Rocky Mountains, U.S.: introduced)	Rapid larval development time, vegetation provides refuge from predation
	T	P	0	Hirner and Cox 2007 (south-central British Columbia, C.A.: introduced)	Small effect of trout or low statistical power
	C	N	-	Pillioid and Peterson 2001 (central Idaho, U.S.: introduced)	Predation on larvae and juveniles
<i>Rana muscosa</i>	T	P	-	Bradford 1989 (eastern California, U.S.: introduced) ; Bradford et al. 1998 (eastern California, U.S.: introduced); Knapp and Matthews 2000 (eastern California, U.S.: introduced); Knapp et al. 2001 (eastern California, U.S.: introduced)	Bradford 1989, et al. 1998, Knapp and Matthews 2000, Knapp et al. 2001: Predation on tadpoles and frogs

Appendix A (cont.)

	T	N	-	Knapp et al. 2001 (eastern California, U.S.: introduced); Vredenburg 2004 ^b (eastern California, U.S.); Finlay and Vredenburg 2007 (eastern California, U.S.: introduced)	Knapp et al. 2001, Vredenburg 2004: Predation on tadpoles; Finlay and Vredenburg 2007: Predation on tadpoles, reduction in prey availability for adult frogs
	J, A	N	-	Vredenburg 2004 ^b (eastern California, U.S.: introduced); Finlay and Vredenburg 2007 (eastern California, U.S.: introduced)	Vredenburg 2004: Predation on tadpoles; Finlay and Vredenburg 2007: Predation on tadpoles, reduction in prey availability for adult frogs
	A	P	-	Knapp and Matthews 2000 (eastern California, U.S.: introduced)	
	C	P	-	Knapp 2005 (eastcentral, California, U.S.: introduced), Davidson and Knapp 2007	
<i>Rana perezi</i>	A	N	0	Martínez-Solano et al. 2003 (northcentral Spain: introduced)	
<i>Rana temporaria</i>	E,T	P	-	Tiberti and von Hardenburg 2012 (western Italian Alps: introduced)	Adult avoidance of ponds with fish or local extinction via predation
	T	P, N	+	van Buskirk 2005 (north-central Switzerland: not specified)	

Appendix A (cont.)

C	P	-	Hartel et al. 2007 (central Romania: combination); Tiberti and von Hardenburg 2012 (western Italian Alps: introduced)
C	P, N	0	Orizaola and Braña 2006 (northern Spain: introduced)

^aThis study introduced fish into breeding ponds and examined correlations between fish presence/absence and anuran abundance.

^bThese studies removed fish from natural water bodies and examined correlations between fish presence/absence and anuran presence/absence or abundance.

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APPENDIX B: CORRELATORY RELATIONSHIPS BETWEEN ANURANS AND NON-FISH PREDATORS⁶

Summary of correlational field studies examining associations between non-fish predators and anuran presence (P) or abundance (N) during egg stage (E) or tadpole stage (T). Negative associations with predators is indicated by – and no association is indicated by 0. Reference includes location of study and status of predator (i.e. introduced predator, native predator, or not specified in the paper). Studies were not included if they did not distinguish specific predators (i.e. study combines multiple species together in the same predator category).

Species	Stage	Method	Predator	Association	Reference	Potential mechanisms proposed by authors
Family Bufonidae						
<i>Epidalea calamita</i>	E, T	P	Crayfish	–	Cruz et al. 2006 (southwestern Spain: introduced)	Predation
Family Hylidae						
<i>Hyla versicolor/chrysosecelis</i> complex	T	N	Crayfish	– (in 2 of 4 years)	Shulse et al. 2013 (northeast Missouri, U.S.: native)	
	T	N	Dragonfly	– (in 1 of 4 years)	Shulse et al. 2013 (northeast Missouri, U.S.: native)	Larvae develop “dragonfly morph” that is less susceptible to invertebrates
<i>Pseudacris maculata</i>	T	N	Crayfish	0	Shulse et al. 2013 (northeast Missouri, U.S.: native)	
	T	N	Dragonfly	– (in 1 of 2 years)	Shulse et al. 2013 (northeast Missouri, U.S.: introduced)	
<i>Pseudacris regilla</i>	E, T	N	Crayfish	–	Riley et al. 2005 (southern California, U.S.: introduced)	Predation
Family Ranidae						
<i>Lithobates clamitans</i>	T	N	Crayfish	–	Shulse et al. 2013 (northeast Missouri, U.S.: introduced)	Predation or adult avoidance

⁶ This material has been published in *BioScience*. Full citation: Buxton, V. L., and J. H. Sperry. 2017. Reproductive decisions in anurans: A review of how predation and competition affects the deposition of eggs and tadpoles. *BioScience* 67:27-38

Appendix B (cont.)

<i>Rana aurora</i>	T	P	Bullfrog	0	Shulse et al. 2013 (northeast Missouri, U.S.: introduced) Adams 1999 (western Washington, U.S.: introduced), Adams et al. 2011 (western Oregon, U.S.: introduced)	
<i>Rana temporaria</i>	E	P	Newt	0	Grözinger et al. 2012 (northern Germany: not specified)	Newts migrate into ponds at the same time or later than frogs

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APPENDIX C: PLAYBACK EXEMPLARS FOR *ANAXYRUS AMERICANUS* AND *HYLA CHRYSOSCELIS*⁷

Details of each exemplar used in playback recordings of *Anaxyrus americanus* and *Hyla chrysoscelis*.

Species	Source	Identifier #	Recordist	General Location	Lat/Lon	# Males
<i>A. americanus</i>	Voices of the Night Audio CD, produced by Cornell Lab of Ornithology	NA	Arthur A. Allen, Peter P. Kellogg	unknown	unknown	single
	Macaulay Library, Cornell Lab of Ornithology	ML183605	Carl H. Gerhardt	Boone County, MO	39.9847114, - 92.44699	single
	Macaulay Library, Cornell Lab of Ornithology	ML53169	Steven R. Pantle	Santa Clara county, NY	44.423215, - 74.419069	multiple
	Macaulay Library, Cornell Lab of Ornithology	ML38828	Elliot Lang	Franklin county, NY	unknown	multiple
<i>H. chrysoscelis</i>	Macaulay Library, Cornell Lab of Ornithology	ML181955	Carl H. Gerhardt	Chatham county, GA	32.005218, - 81.2844086	single
	Macaulay Library, Cornell Lab of Ornithology	ML183617	Carl H. Gerhardt	Stoddard county, MO	37.023488, - 90.1143265	multiple
	Macaulay Library, Cornell Lab of	ML183759	Carl H. Gerhardt	Chatham county,	32.0357824, -	single
	Macaulay Library, Cornell Lab of Ornithology	ML185098	Carl H. Gerhardt	Dent county, MO	37.456328, - 91.667404	multiple
	Macaulay Library, Cornell Lab of Ornithology	ML176296	Geoffrey A. Keller	Brown county, IN	39.2132295, - 86.2079573	multiple

⁷ This material has been published in *Behavioral Ecology*. Full citation: Buxton, V. L., M. P. Ward, and J. H. Sperry. 2015. Use of chorus sounds for location of breeding habitat in 2 species of anuran amphibian. *Behavioral Ecology* 26: 1111-1118.