



Behavioral Ecology (2015), 00(00), 1–8. doi:10.1093/beheco/arv059

Original Article

Use of chorus sounds for location of breeding habitat in 2 species of anuran amphibians

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Received 2 January 2015; revised 18 March 2015; accepted 30 March 2015.

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 tree frogs (*Hyla chrysoscelis*) to determine whether toads and tree frogs 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. *Anaxyrus 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.

Key words: *Anaxyrus*, breeding behavior, chorus sounds, conspecific attraction, *Hyla*.

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 nonrandom, 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 toward 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

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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. This has been the case with songbirds, where broadcasting playbacks of conspecific song in suitable but unoccupied habitats acts 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. 2010). 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 2009), 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 toward 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 tree frogs (*Hyla chrysoscelis*), gray tree frogs (*Hyla versicolor*), barking tree frogs (*Hyla gratiosa*), and male wood frogs (*Rana sylvatica*) have all been found to approach recordings of a conspecific chorus, though green tree frogs (*Hyla cinera*) have been observed as unresponsive (Gerhardt and Klump 1988; Bee 2007; Swanson et al. 2007; Christie et al. 2010). These studies suggest that it may be beneficial for anurans to orient toward 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 tree frogs (*Hyla arenicolor*), but failed to find supporting evidence for bird-voiced tree frogs (*Hyla avivoca*), and suggested that

these differential responses may be due to life-history characteristics. *Hyla arenicolor* breed in unpredictable, ephemeral streams and have low philopatry, whereas *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. *Anaxyrus americanus* are typically explosive breeders, with peak reproductive activity generally lasting from less than a week to 4 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* have 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). *Hyla chrysoscelis* are prolonged breeders, with breeding lasting from 2 to 4 months throughout their range (Ritke et al. 1990). *Hyla chrysoscelis* exhibits a lek-like breeding system, where males call nightly from ponds and females choose males and initiate amplexus. *Hyla chrysoscelis* breeds in a variety of habitats including includes 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 man-made pond, whereas *H. chrysoscelis* breeding took place over the course of 3 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 man-made pond, but were not observed breeding in the seasonal

wetlands, whereas *H. chrysoscelis* exhibited the opposite pattern. In March 2014, we installed 18 artificial garden ponds (1.7 m × 1.2 m, 91 gallon capacity) in a grid throughout the study area. Ponds consisted of a flexible polyethylene pond liner with 2 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 branches 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 9 randomly selected artificial playback ponds (Figure 1a). The remaining 9 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 1–2h before sunset until midnight, with 15 min of silence after 60 min 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 Supplementary Data for further details). Each exemplar was clipped to 2 min and repeated 6 times on a 60-min track. When *A. americanus* were no longer heard calling from the natural surrounding ponds, we rerandomized playback and control locations and began broadcasting *H. chrysoscelis* calls (Figure 1b). Similarly, vocalization tracks consisted of 5 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 tree frog 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 3 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 (VIE) injected in the hindlimbs (Northwest Marine Technologies, Inc.). We opportunistically monitored ponds during evenings and nights for any anuran activity

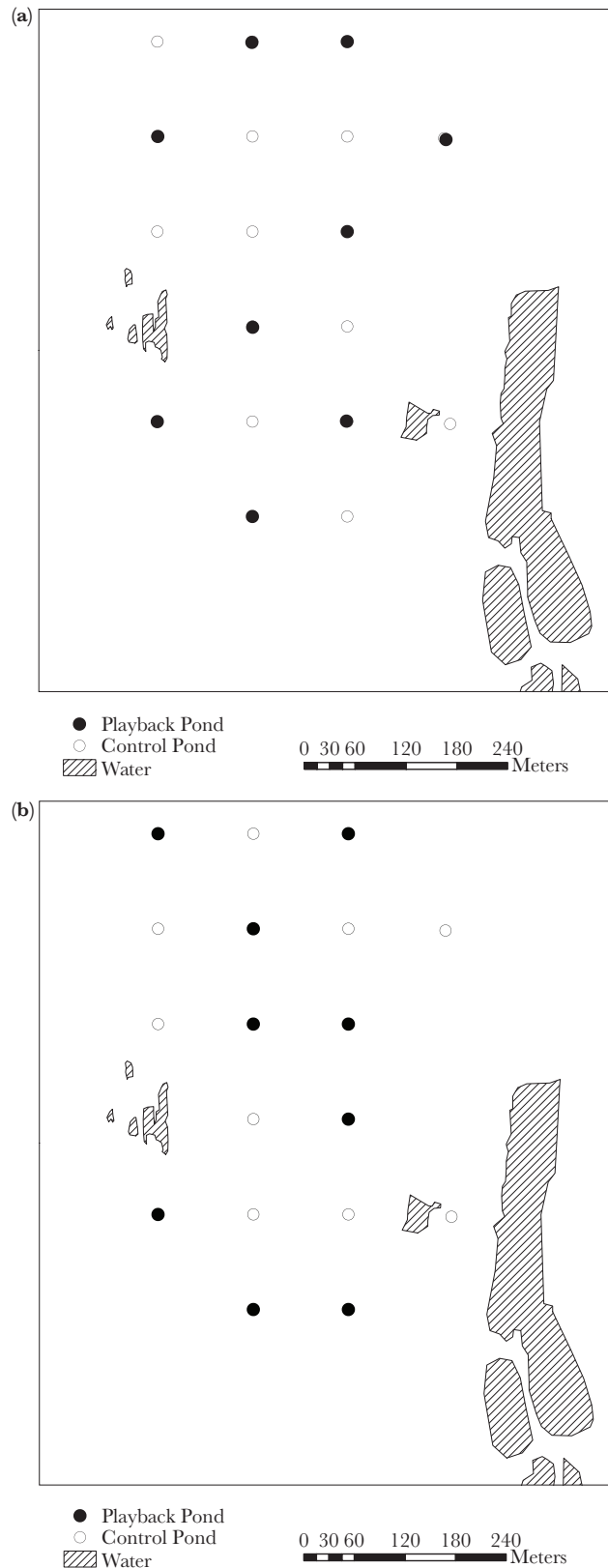


Figure 1 Locations of experimental ponds at Camp Atterbury Joint Manuever Training Center in central Indiana for (a) *Anaxyrus americanus* and (b) *Hyla chrysoscelis*. Black circles indicate treatment ponds with conspecific playback and white circles indicate silent control ponds.

such as calling males and mating pairs. We captured and marked individuals seen at ponds using VIE and visible alphanumeric tags (VIA; Northwest Marine Technologies, Inc.). We removed hetero-specific males from playback ponds and returned these individuals to the man-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 Fischer'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 tree frog capture rate (captures/night) at treatment and control ponds. All analyses were conducted in Program R (R Development Core Team 2010).

RESULTS

Anaxyrus 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 1-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 ($P = 0.015$; Figure 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 ($\chi^2 = 7.9$, $df = 1$, $P = 0.005$; Figure 3). The first oviposition event occurred in a playback pond after 7 days of playbacks, whereas 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 1 playback pond containing 9 oviposition events, each on different days.

Over the course of 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 6 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. Over the course of 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. *Hyla chrysoscelis* exhibited strong conspecific attraction, finding and colonizing playback ponds faster and more often than controls, whereas *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, whereas *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 1-week span in mid-April), any prospecting of new and unknown breeding locations may put them at risk of missing their short reproductive window. *Hyla 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 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. Although 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.

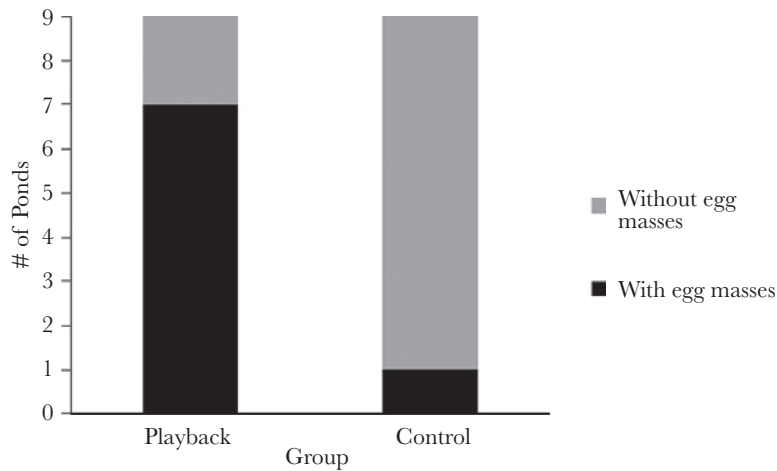


Figure 2
Number of playback and control ponds found with egg masses for *H. chrysoseleis*.

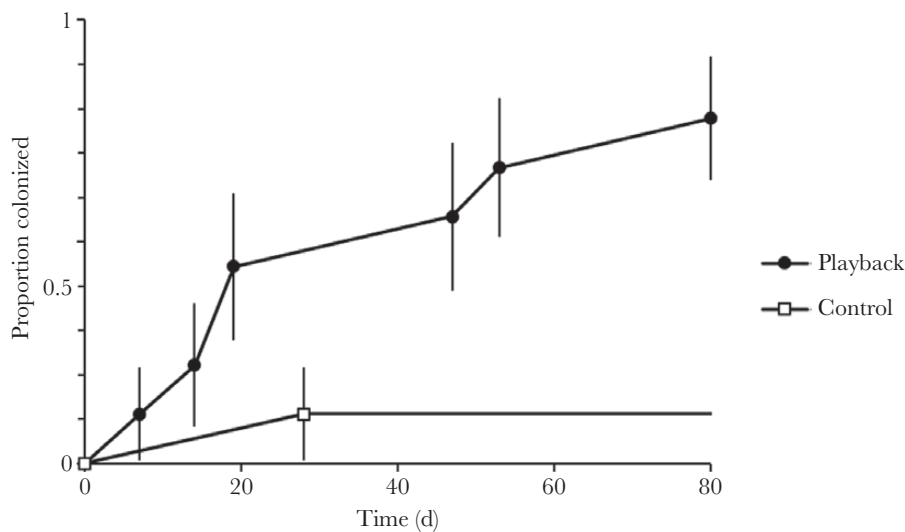


Figure 3
Time in days (d) until first colonization (i.e., oviposition event) of ponds by *H. chrysoseleis* represented by survival curves. Each point represents an initial oviposition event with associated standard error bars.

An additional consideration not addressed in this study is whether *H. chrysoseleis* 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 toward 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 toward artificial chorus-shaped noise in the phonotaxis arena, whereas *H. chrysoseleis* females only oriented toward natural chorus noises, suggesting that toads may be less selective to a stimulus. Orienting toward 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 toward 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 toward any perceived sound. In our study, we did not observe species other than *H. chrysoseleis* 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 has 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

conspicuous cues, for dispersing *H. chrysoscelis*. 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. chrysoscelis* use calls to locate breeding ponds. Because we did not know the initial starting point of *H. chrysoscelis* in the landscape, we could not determine distances at which tree frogs use acoustic call to orient. Swanson et al. (2007) reported that female *H. chrysoscelis* 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 tree frog 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. chrysoscelis*.

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. Although 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. Although 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.

Although 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

(Hopey and Petranka 1994), and mountain chorus frogs (*Psuedacris brachyphona*) preferentially select breeding ponds within forested areas (Felix et al. 2010). Although 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. chrysoscelis* 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 whereas males were located 30 m, indicating that it is not uncommon for tree frogs to make short-distance forays into terrestrial habitat. We found *H. chrysoscelis* and reproductive activity at artificial ponds located up to 345 m from natural tree frog breeding areas, and also observed that the pond with the highest number of oviposition events was located 261 m from the closest natural tree frog 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 tree frog breeding activity occurred in artificial ponds within 15 m of the natural breeding pond. This result may be due to the lack of social cues at distant breeding ponds, leading to decreasing probability of colonization as distances from natural breeding ponds increased. 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 interpond distance may not represent as significant of a barrier to colonization than previously perceived. Thus, our study demonstrates that gray *H. chrysoscelis* 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 tree frog 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). Although 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.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at <http://www.beheco.oxfordjournals.org/>

FUNDING

Funding was provided by the Construction Engineering Research Laboratory of the Engineer Research Development Center (grant number W9132T-15-0004).

We thank Camp Atterbury Joint Manuever Training Center for hosting this research, with tremendous thanks to D. Slack. Thanks to J. Rabideau for assisting with data collection. Thanks to B. DeGregorio and 2 anonymous reviewers for providing feedback on the manuscript. Animal procedures conformed to the permit approved by the University of Illinois (IACUC #14021).

Handling editor: Bob Wong

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