

PHONOTACTIC RESPONSE OF JUVENILE COPE’S GRAY TREEFROGS (*HYLA CHRYSOSCELIS*) EXPOSED TO CONSPECIFIC AND HETEROSPECIFIC ACOUSTIC SIGNALS

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Abstract.—Anurans use auditory cues, including male calls, for orientation and movement in the environment. Whereas previous research has focused on the phonotactic response of breeding adults to calls, the response of recently metamorphosed anurans has not been tested. We assessed the phonotaxis of 144 juvenile *Hyla chrysoscelis* (Cope’s Gray Treefrogs) of two size classes to choices between silence, conspecific, or heterospecific *Hyla versicolor* (Eastern Gray Treefrog) cues in an experimental setting using an artificial arena. We found no significant response to either call type for either size class. Our results do not support the hypothesis that treefrogs orient toward or away from male calls shortly after metamorphosis.

Key Words.—auditory cues; orientation; movement; anuran; calling

INTRODUCTION

Dispersal is a vital ecological process that has important consequences for both individual fitness and population-level processes (Baguette et al. 2013). Whether an individual makes an initial directed dispersal movement (Pittman et al. 2014) may depend on both external factors and internal state (Nathan et al. 2008; Clobert et al. 2009). External factors that may influence movement include biotic and abiotic environmental stimuli such as slope, cover, and optimal microclimate (Nathan et al. 2008). Moreover, responses to external cues can be influenced by the internal state of an individual, derived in part from differences in physiology, morphology, and life-history traits (Clobert et al. 2009), creating differences in choice of movement even when faced with the same stimuli. For this reason, understanding how movement choice responses are affected by external factors, phenotypic differences, and their interaction may help us understand what factors drive initial orientation and dispersal (Gerhardt et al. 1994; Cowen and Sponaugle 2009).

Acoustic signals are one set of external factors that can influence individual movement and dispersal (Nathan 2008). Conspecific signaling has been shown to influence individual dispersal in a wide range of species (Stamps 1987; Gautier et al. 2006; Pizzato et al. 2016), and individuals may use acoustic signals from conspecifics and heterospecifics to reduce uncertainty in habitat quality and resource acquisition as a part of soundscape orientation (Danchin et al. 2004; Valone 2007; Slabbekoorn and Bouton 2008; Fletcher and Sieving 2010). Adult anurans can exhibit positive

phonotaxis towards conspecific chorus when presented with con- and heterospecific cues during mate selection and reproduction (Gerhardt and Klump 1988; Bee 2007) and eavesdropping on heterospecific calls has also been documented (Phelps et al. 2007). It is not clear, however, if juveniles use the same cues for orientation when leaving the natal pond, or at what developmental point an individual becomes responsive to conspecific calls/choruses (Gerhardt and Bee 2007). Juvenile dispersal is a growing area of interest because the maintenance of anuran populations is dependent on successful dispersal, and juveniles appear to be the primary long-distance dispersers (Pittman et al. 2008). Little research has been done, however, to uncover the factors influencing initial movement towards a habitat (Pittman et al. 2014), though habitat type does seem to affect initial orientation and movement in some species (Rothermel and Semlitsch 2002; Patrick et al. 2007). To the best of our knowledge, there are no tests of phonotaxis in juvenile frogs towards conspecific or heterospecific calls.

While ear development is incomplete for some species of anurans at metamorphosis (Heatherington 1987), there is evidence that even at this stage juveniles can perceive sound waves propagated through the air (Katbamna et al. 2006; Boatright-Horowitz and Simmons 1995), though perhaps at a shifted frequency range relative to the adult stage (Katbamna et al. 2006). Additionally, whereas there might be tympanic deafness at some point, it has been shown to recover by Gosner stage 45 (Gosner 1960) in bullfrogs (tested via tympanic stimulation, Boatright-Horowitz and Simmons 1997). Though the exact timing of development of auditory senses is not fully understood in all species, there is

evidence that airborne sound may be perceivable at and immediately following metamorphosis in some species of anurans.

As acoustic signals represent one potentially important external factor that influences movement, body size, an internal state, also affects individual movement and orientation (Bowler and Benton 2005). In amphibians, smaller body size is associated with a higher risk of dispersal mortality via desiccation and predation (Werner 1986), which may result in larger individuals being more likely to disperse. Due to these risks, body size may be an important factor in predicting juvenile dispersal away from a natal pond or the likelihood of philopatry (Semlitsch 2008; Child et al. 2009). Consequently, body size may affect the phonotactic response of a juvenile to acoustic signals as a result of differences in desiccation and predation risks, generating a different orientation choice at different body sizes.

Hyla chrysoscelis (Cope's Gray Treefrog) is a nocturnally breeding species found throughout the eastern U.S. (Ritke et al. 1990). Adult *H. chrysoscelis* have been used in multiple acoustic playback experiments and exhibit phonotaxis towards conspecific cues when selecting a breeding habitat (Swanson et al. 2007; Buxton et al. 2015; Vélez et al. 2017). The range of *H. chrysoscelis* overlaps in many areas with its sister taxon, *H. versicolor* (the tetraploid Gray Treefrog), a very similar species distinguishable principally by call (Gerhardt et al. 1994). While no study of juvenile dispersal has been conducted in *H. chrysoscelis*, *H. versicolor* engages in dispersal movements post metamorphosis (Roble 1979). Though individuals move away from the natal pond at this stage, and do not immediately move to a different pond, but rather forested habitat, juveniles could use the soundscape of calls from surrounding ponds to navigate sub-optimal matrix habitat toward suitable habitat. Whereas no studies have explicitly tested juvenile auditory sensitivity in *H. chrysoscelis* or *H. versicolor*, *H. versicolor* calls overlap the detectable range for juveniles of other species (1–3 kHz; Schofner and Feng 1981; Gerhardt and Schul 1999; Katbamna et al. 2006; Gerhardt 2008), and differences between the two calls are due primarily to variance in call pulse rate (Gerhardt 2005) rather than a difference in frequency. Furthermore, *H. chrysoscelis* are considered prolonged breeders (Buxton et al. 2015) with a breeding season of 4 mo or longer during which a female may mate up to three times (Ritke et al. 1990; McCauley et al. 2000), and thus juveniles of the species may reasonably hear adult calls upon metamorphosis.

In this experiment, we tested the phonotactic response of two size classes (small versus large) of recently metamorphosed juveniles of *H. chrysoscelis* to conspecific and heterospecific (*H. versicolor*) natural

chorus recordings. Using both single-stimulus and double-stimuli trials, we recorded the phonotaxis of individuals when presented with a conspecific chorus, a heterospecific chorus, and/or silence. We hypothesized that individuals would respond to auditory stimuli and we predict that they would exhibit positive phonotaxis towards a conspecific or heterospecific stimulus when given a choice between the chorus and silence. When given a choice between heterospecific or conspecific cues, we predict the individuals would orient towards conspecific cues. Additionally, we hypothesized that size of frogs affects phototaxis and we predict that larger individuals would be more likely to make a choice and orient themselves towards either side of the arena than smaller individuals.

MATERIALS AND METHODS

Collecting.—We collected *H. chrysoscelis* eggs from about 10 clutches at the experimental pond facility at the Ecology Research Center (ERC) of Miami University in Oxford, Ohio, USA, on 14 May 2018; this area is located in an open field near a secondary forest. Eggs hatched in a 1,000 L artificial mesocosm containing 1 kg of deciduous leaf litter, and algae and zooplankton inoculate from a nearby pond at the ERC. After the eggs hatched, we transferred the tadpoles (Gosner stage 25, Gosner 1960) to similarly prepared mesocosms at the ERC in either a high-density environment with 60 tadpoles or a low-density environment with 20 tadpoles, to generate size class differences (Semlitsch and Caldwell 1982). Upon tadpole metamorphosis (20–30 June 2018) determined by the emergence of one or both forelimbs (Gosner stage 42, Gosner 1960), we removed individuals from the mesocosm and held them in the lab until tail resorption (Gosner stage 46). We held up to 12 individuals in soil-bottomed terraria (15 × 15 × 40 cm) at 23° C until they were used for trials (up to five weeks). We fed all individuals crickets *ad libitum* in terraria until used for trials. To verify that we generated two distinct size classes for individuals through the density treatments, we compared mean size for each treatment using Analysis of Variance (ANOVA) after confirming normality and homoscedasticity. Treefrogs reared in high-density mesocosms (mean = 0.46 ± [standard error] 0.010 g) were 28% smaller than those reared in low-density treatments (mean = 0.63 ± 0.014 g; $F_{1,136} = 10.81$, $P < 0.001$) at metamorphosis.

Experimental set-up.—To conduct behavioral choice trials, we built a 3.66 × 0.61 × 0.61 m enclosure (Fig. 1) in a greenhouse (26° C, ambient light) on the campus of Miami University from polyvinyl chloride sheets (bottom) and corrugated plastic (walls) with a strip of plastic mesh along the top to prevent escape.

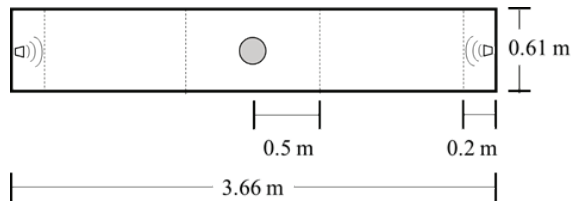


FIGURE 1. Diagram of the enclosure for playback tests for *Hyla chrysoscelis* (Cope’s Gray Treefrog). Key features include the release point as shown by a circle in the center, the speakers at either end, the inner dotted lines representing the no-movement lines, and the outer dotted lines representing the choice lines.

We placed two programmable Icotec GC350 speakers (Icotec, Holland, Ohio, USA; frequency response approximately 150 Hz to 5 kHz) inside of the enclosure on opposing ends. The sound pressure was equalized for both speakers to 82 dB sound pressure level using a Digital Sound Level meter (RisePro, Phoenix, Arizona, USA), which is A Frequency weighted and fast Root Mean Squared time weighted with a reference of 20 μ Pa. This device was held in the center of the enclosure equidistant from each speaker before every trial. We set up a HandyCam™ (Sony, Tokyo, Japan) above the center of the enclosure to track movement of each individual.

Playback tests.—We conducted behavioral trials between 1500 and 2100 from 2 July 2018 until 6 August 2018. For each trial day, we weighed individuals to be tested using a bench scale (Sartorius AG, Göttingen, Germany; resolution 0.001 g), and transported them to the test site. We provided each individual with either a single-stimulus or double-stimulus choice. We exposed individuals given a single stimulus choice to a randomly assigned speaker broadcasting either a conspecific (*H. chrysoscelis*) chorus or a heterospecific (*H. versicolor*) chorus with the other speaker broadcasting silence. We used recordings of natural, low-density choruses for both species that had been recorded and catalogued by the Amphibian Research and Monitoring Initiative, U.S. Geological Survey, Midwest Region, La Crosse, Wisconsin, USA. We chose low density choruses, as they better represent late-season chorus strength (Runkle et al. 1994; Bertram et al. 1996). For individuals given a double-stimulus choice, we exposed frogs to one randomly assigned speaker broadcasting the conspecific chorus and the other broadcasting the heterospecific chorus. We randomly assigned individuals to one of the three trial types, alternating by size class with each successive trial. We used each individual for only one trial. We tested 63 large size class individuals and 81 small size class individuals, with approximately one third of each size class per choice combination. Of the 144 total trials run for *H. chrysoscelis* individuals, six individuals escaped during the test.

At the start of each trial, we placed one individual under a small container inside the enclosure and started the appropriate chorus recordings. Following a 1-min acclimation period, we used a rope and pulley system to release each individual into the enclosure to reduce movement bias due to researcher presence (Ryan and Rand 2003). We marked 20 cm from the speaker and declared that a choice was made if the individual crossed the 20-cm mark close to a speaker (Straughan 1975; Ursprung et al. 2009). We allowed the individual 20 min to move about the enclosure and recorded the choice at that time. If an individual did not move more than 0.5 m from the center, we declared the individual did not move from center. We removed the individual and wiped the bottom of the enclosure with a 30% ethanol solution to remove potential chemosensory stimuli.

Analysis.—To confirm no bias in movement of the individuals toward a particular enclosure side, we used a Chi-square test (test of equal proportions) to compare both final choice between the two sides of the enclosure (right or left), as well as time spent per enclosure side. We analyzed individual choice for acoustic stimuli (heterospecific, conspecific, or silence) by Chi-square test with a 95% confidence interval (Gerhardt 1995), and time spent on either enclosure side using a paired *t*-test. As all three options are not available to each individual, we analyzed each choice pair separately for each size class. To test whether or not body size influenced movement, we used Chi-square tests to compare type of response (no movement, movement without choice, movement with choice) with size class. Among those individuals that made a choice, we also used a Chi-square test to assess the influence of size class with choice of stimulus. We used $\alpha = 0.05$ for all statistical analyses and we completed all analyses in R version 3.6.1 (R Core Team 2019).

RESULTS

Of the 138 juveniles tested, we found that 29 (21%) did not move more than 0.5 m, 46 (33%) moved but did not make a choice (i.e., approach a speaker closer than 20 cm), and 63 (47%) made a choice. These ratios were similar across the three test categories (silence vs. conspecific; silence vs. heterospecific; conspecific vs. heterospecific). We only used those 63 trials when we assessed choice (Table 1).

We tested for bias in choice between the left and right side of the enclosure, but found no significant differences in final choice ($\chi^2 = 1.29$, $df = 1$, $P = 0.257$) or the total time spent ($t = 1.969$, $df = 136$, $P = 0.179$) on either side. This result indicates no bias in our trials for the right versus left side of the enclosure. Treefrogs showed no significant preference for either treatment in

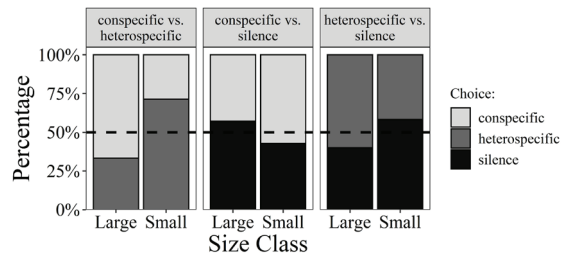


FIGURE 2. Percentage of individual *Hyla chrysoscelis* (Cope's Gray Treefrog) from each size class per choice test that oriented toward each stimulus (sample sizes found in Table 1). A dashed line is given at 50% to reference what would be expected by chance.

the double-stimulus trial (conspecific vs. heterospecific; $\chi^2 = 0.80$, $df = 1$, $P = 0.371$), or either single-stimulus trial with silence vs. conspecific ($\chi^2 = 0.48$, $df = 1$, $P = 0.827$) or silence vs. heterospecific ($\chi^2 = 0.00$, $df = 1$, $P = 1$; Table 1). Body size did not affect movement response of treefrogs in this study ($\chi^2 = 2.84$, $df = 2$, $P = 0.242$). Additionally, for treefrogs that made a choice, body size did not affect choice preference ($\chi^2 = 1.90$, $df = 3$, $P = 0.594$; Fig. 2).

DISCUSSION

Juveniles are believed to be the predominant life stage in anurans that disperse from natal to novel habitat (Semlitsch 2008; Pittman et al. 2014). Chorusing at nearby ponds could serve as impetus for movement toward future breeding habitat, or be used to navigate through sub-optimal matrix habitat toward suitable non-breeding habitat, particularly when species have prolonged breeding, such as in *H. chrysoscelis* and *H. versicolor*. We did not test either of those specific hypotheses here; we wished only to assess if juvenile *H. chrysoscelis* exhibited a selective movement response to these sounds, and if differences in body size changed these responses. We found, however, that *H. chrysoscelis* juveniles did not orient toward or away from either conspecific or heterospecific auditory cues regardless of the size of individuals. Our study suggests that acoustic cues are not a significant motivating factor of movement for *H. chrysoscelis* juveniles.

There are several other hypotheses regarding which factors cue juvenile movement or dispersal, which include the following: olfactory cues (Ogurtsov 2004),

moving when desiccation risk is low (Child et al. 2008), and orienting toward specific habitat (Rothermel and Semlitsch 2002; Walston and Mullin 2008; Youngquist and Boone 2014). Given the influence of habitat on initial orientation following juvenile emergence, the orientation and movement of newly metamorphosed individuals in subsequent stages of movement may be strongly affected by other landscape cues, such as elevation, moisture, and canopy cover (Walston and Mullin 2008; Haggerty et al. 2019). In treefrog species specifically, juveniles may not use calls for orientation due to strong selection for arboreal habitat on leaving the natal pond and when not actively breeding (Johnson et al. 2008). In effect, these other factors may be more important to juvenile frog survival and growth than future prospects at nearby ponds. While our usage of a uniform arena allowed us to test for auditory response while mitigating environmental factors, it is possible that if juveniles use auditory cues to orient toward suitable habitat from sub-optimal habitat, juveniles do not require auditory navigational cues while in a uniform environment. Future research using a more complex arena could address this hypothesis and potentially yield differing results from our study.

Beyond any specific external cue, life stage may play an important role in the responsiveness of anurans to acoustic cues. Whereas many species will show positive phonotaxis towards social acoustic cues during the mating season (Bee 2007; Shen et al. 2008; Christie 2010), some species like female Green Treefrogs (*Hyla cinerea*) show no preference for social acoustic signals outside of their breeding season (Höbel and Christie 2016), suggesting that orientation towards acoustic cues may be limited to searching for a mate or finding sites at reproductive maturity. Juveniles in our study may not have shown movement toward or away from cues because of the life stage and time of testing, which ranged for a few days up to five weeks after metamorphosis. While we tested individuals by metamorphosis date (e.g., individuals that metamorphosed earlier were used earlier in trials), we cannot account for differences in age and developmental stage during this period. Potentially, the ability of an anuran to use social cues to find a habitat is triggered during the breeding season and is not manifested in juvenile behavior, which would explain the lack of choice demonstrated by our study.

TABLE 1. Choice results showing number of individuals by trial type and body size of *Hyla chrysoscelis* (Cope's Gray Treefrog). Trial types were conspecific vs. heterospecific (labeled columns 1–3), conspecific vs. silence (columns 4–6), and heterospecific vs. silence (columns 7–9).

	Con-specific	Hetero-specific	No Choice	Con-specific	Silence	No Choice	Hetero-specific	Silence	No Choice
Large	4	2	13	3	6	14	6	4	6
Small	4	10	14	8	4	12	5	7	14
Total	8	12	27	11	10	26	11	11	22

Although there is evidence in other species that juveniles of this development stage can hear airborne sounds (Schofner and Feng 1981; Boatright-Horowitz and Simmons 1995; Katbamna et al. 2006), in some species (especially smaller species such as Spring Peepers, *Pseudacris crucifer*), the middle ear tympanic pathway does not fully develop until 60 d post-metamorphosis (Hetherington 1987). Lack of fully developed airborne auditory receptors could limit the responsiveness of juveniles to airborne cues immediately post metamorphosis (Boatright-Horowitz and Simmons 1997). Even so, the opercularis system has been shown to be developed at this stage (Hetherington 1987). Whereas in some cases this is thought to enable the detection of only vibrations sensed via contact with a substrate, other evidence indicates that this system allows for receptivity of airborne sounds up to 2.5 kHz (Hetherington 1992; Simmons and Horowitz 2007). Furthermore, there is evidence that a lung-based system of hearing exists in a species lacking a tympanic membrane, introducing the possibility of detection of airborne sound even without a fully developed tympanic-stapes complex (Hetherington and Lindquist 1999). Nevertheless, the specific auditory system of *H. chrysoscelis* has not been examined, and it is possible that a lack of receptivity to airborne sound at this stage could result from an undeveloped auditory system. Future research testing the auditory system in juvenile treefrogs could address the question of auditory sensitivity and inform further stage-based examinations of phonotaxis.

Whereas other factors influencing juvenile anuran movement and orientation have been previously examined, to our knowledge this is the first examination of auditory cues on phonotaxis in recently metamorphosed juveniles: the life stage that has been found to be the most likely to disperse from natal sites. While we did not find a significant effect of chorusing on movement, we highlight the potential role the auditory environment could have on emerging anurans, while simultaneously discussing several potential reasons for the lack of response in our study. Further exploration and clarification of the factors that influence movement to new habitats will allow us to untangle juvenile movement, identify potential barriers for dispersal, and infer dispersal routes between breeding sites.

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(not pictured)

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