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Do Green Treefrogs Use Social Information to Orient Outside the Breeding Season?

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Gerlinde Höbel and Ashley Christie (2016) To decide efficiently where to forage, rest or breed, animals need information about their environment, which they may gather by monitoring the behavior of others. For example, attending to the signals of conspecifics or heterospecifics with similar habitat requirements may facilitate habitat choice. Such social information use seems taxonomically widespread, yet there is currently a dearth of information for amphibians. Anuran amphibians, with their highly developed auditory system and robust phonotaxis towards advertisement calls when searching for mates seem predisposed to use this hearing capability in other behavioral contexts. We conducted playback experiments to test whether anurans exploit acoustic signals in a non-reproductive context. In our experiments female Green Treefrogs did not show phonotaxis to signals associated with the presence of other frogs, and the orientation and speed of their movement was not different from animals randomly moving inside a silent arena. Previous studies documenting social information use in anurans have tested reproductively active frogs during the breeding season. By contrast, our study examined non-reproductive animals, and these did not approach social signals. We propose two non-exclusive hypotheses for this observed difference in phonotaxis behavior: (1) attending to social signals is restricted to ecologically most relevant time periods in a frogs life (*i.e.*, finding breeding sites during the mating season), or (2) the ability of acoustic signals to stimulate the auditory system may be influenced by hormone levels regulating the reproductive state.

Key words: Acoustic communication, Anura, Amphibians, Phonotaxis.

BACKGROUND

Animals must decide where to forage, rest or breed, and to decide efficiently they need information about their surroundings (Shettleworth 2010). They can acquire this information by personally sampling the environment, or they may gather social information by monitoring the behavior of other individuals residing in the environment (Danchin et al. 2004; Bonnie and Earley 2007). A rapidly growing literature shows that social information use is taxonomically widespread (Rieucau and Giraldeau 2011), and that animals use social information in a range of ecological contexts including foraging, anti-predatory behavior, agonistic interaction, mate choice and breeding habitat selection (summarized in Giraldeau et al. 2002; Valone 2007; Rieucau and Giraldeau 2011).

Anuran amphibians (frogs, toads) are a major study group for investigating the ecology and evolution of acoustic communication (Ryan 2001; Gerhardt and Huber 2002). Anuran vocalizations are conspicuous and diverse (Toledo et al. 2015). Because most of their vocal activity is concentrated in the breeding season, the majority that is known about anuran acoustic behavior is related to reproduction, primarily mate choice and sexual selection (Ryan 2001; Gerhardt and Huber 2002; Wells 2007; Yasumiba et al. 2015), male territoriality (Wilczynski and Brenowitz 1988; Wagner 1989; Bee and Gerhardt 2002), and

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breeding habitat choice (*i.e.*, Resetarits and Wilbur 1989; Binckley and Resetarits 2002; Rieger et al. 2004; Buxton et al. 2015).

The breadth and depth of information on anuran behavior associated with reproduction is contrasted by an almost complete lack of information on the non-breeding-season activities of most species. We know, for example, comparatively little about where they spend the time between breeding seasons (Ritke and Babb 1991; Horn et al. 2005; Johnson et al. 2007), or whether they respond to acoustic cues in the environment outside the reproductive context (Leary and Razafindratsita 1998; Grafe et al. 2002; Höbel et al. 2014).

Whether anuran amphibians use conspecific cues to aid in dispersal and habitat selection during the non-breeding season, for example, is currently unknown. Many anuran species produce vocalizations outside the reproductive period, and from locations away from the breeding ponds (Toledo et al. 2015 and references therein, pers. obs.). These calls are generally referred to with respect to the locations or contexts they occur in: rain calls (given during conditions of high humidity; Goin and Goin 1957), tree calls (given high in the trees where frogs spend the day; Pettus 1955; Blair 1958), or dryland calls (given in retreats away from the breeding pond; Davidson 2014). These calls are structurally very similar to the species' advertisement calls, suggesting they carry species-specific information (Pettus 1955; Goin and Goin 1957; Blair 1958; Bogert 1960; Davidson 2014; Toledo et al. 2015). Consequently, anurans have acoustic cues available that indicate the presence and location of conspecifics in the environment, which may provide valuable information regarding good quality habitat. We conducted playback experiments to test whether Green Treefrogs attend to such social acoustic cues during the non-breeding season.

MATERIALS AND METHODS

Study species and study site

Green Treefrogs (*Hyla cinerea*) are widespread and common in the southeastern United States (Conant and Collins 1998). Their communication system (Gerhardt 1982; Höbel and Gerhardt 2003) and reproductive behavior (Garton and Brandon 1975; Perrill et al. 1978; Mitchell and Miller 1991; Gunzburger 2006) are well studied. They inhabit a variety of wetland ecosystems (Conant and Collins 1998). Across-year capture patterns suggest that there are two periods of increased movement activity, one in spring towards breeding ponds, and one in late fall presumably towards winter retreats (Boughton et al. 2000; Zacharow et al. 2003). Adults are frequently observed using PVC pipe refugia, suggesting that they use tree holes as retreats (Boughton et al. 2000). Frogs frequent PVC pipes during dry or cold weather, especially during the winter months (Zacharow et al. 2003), suggesting that they may overwinter in tree holes/ pipe refugia. Frogs may share adjacent refugia (PVC pipes in pipe bundles; Martin et al. 2004).

The Green Treefrogs (*Hyla cinerea*) used in this study had been collected as sexually mature adult females in the wild (for another experiment), and had been in captivity at the University of Wisconsin - Milwaukee (UWM) for 8 months by the time the trials were conducted. Frogs were housed in glass terraria under 12 h L/D cycle and fed live house crickets (*Acheta domesticus*) twice a week *ad libitum* (Fluker's Cricket Farm, Baton Rouge, LA). The time of year during which we conducted the experiments did not correspond to the species' breeding season, and none of the frogs were in reproductive condition (no eggs/large follicles visible through ventral skin).

Experimental Design

To test the social information use hypothesis, we established four treatments: playback of conspecific call (Con), playback of heterospecific call (Het), playback of white noise (N), and silence (S). Choruses only form during the breeding season, but individual males call sporadically during most of the year (Pettus 1955; Goin and Goin 1957; Blair 1958; Bogert 1960; Davidson 2014; Toledo et al. 2015, pers. obs.). Since we were interested in social information use unrelated to mating, we chose to use a single frog's calls rather than those of a full chorus as the treatment stimuli. We used a custom MATLAB (MathWorks, Natick, MA) program to generate frog call stimuli. Synthetic calls have been shown to be attractive to female frogs (*i.e.*, Gerhardt 1992; Höbel and Gerhardt 2003). The conspecific call stimulus was modeled after an average Green Treefrog (*Hyla cinerea*) advertisement call. It had a duration of 150 ms, a rise time of 25 ms, a fall time of 50 ms, and was repeated every 800 ms. The frequency components of the conspecific stimulus were 900

+ 2700 + 3000 Hz. The heterospecific call stimulus was modeled after an average Barking Treefrog (*Hyla gratiosa*) advertisement call. Like the conspecific stimulus, the heterospecific stimulus had a duration of 150 ms, a rise time of 25 ms, a fall time of 50 ms, and was repeated every 800 ms. The frequency components of the heterospecific stimulus; however, were 500 + 1500 + 2000 Hz. We chose Barking Treefrogs as the heterospecific stimulus because both species have similar habitat requirements and overlap in parts of their range (Conant and Collins 1998), and because gravid green treefrog females discriminate against Barking Treefrog calls in favor of conspecific ones when given a choice, but frequently approach them if presented alone (Oldham and Gerhardt 1975; Höbel and Gerhardt 2003). The white noise stimulus was generated using Adobe Audition 2.0 software (Adobe Systems Incorporated, San Jose, CA, USA). For the white noise stimulus we chose to use a continuous signal with no pauses over a noise stimulus with temporal characteristics of advertisement calls (*e.g.* same duration, repetition rate) to make noise and call stimuli maximally different. During a previous experiment, all females had been tested for their responses to conspecific and heterospecific (Barking Treefrog) calls. Thus, both frog call stimuli used in the present experiment were not completely novel to them, but they had not been exposed to frog calls (either con- or heterospecific) for the past eight months.

Test Procedure

We tested frogs (*n* = 38) in a no-choice paradigm, where one stimulus is presented at a time. Trials were conducted in darkness and there was a 1-min acclimation period during which the frog was restraint inside the release box, as is customary for trials with nocturnal frogs (*i.e.*, Bee 2007). Treatment stimuli were presented in random order with a minimum of 5 min rest between them.

Experiments took place in a circular arena (2 m diameter) set up inside a semi-anechoic chamber at UWM. The arena was delimited by cloth-covered wire mesh, and divided into 24 15° arcs. The speaker broadcasting the stimuli (JBL Control 1Xtreme, Harman International Industries, Inc., Stamford, CT, USA) was placed on the floor just outside the arena. The position of the speaker was changed after every trial, and we used a random number generator to determine the position of the speaker (on a four point scale of East, South, North and West). Stimuli were broadcast using Audacity Ver. 1.2.5 software (Carnegie Mellon University, Pennsylvania, USA) and a Pyle Pro PT1200 amplifier. The sound pressure level (SPL) of the stimuli was adjusted to 85 dB using a sound level meter (Extech Instruments 407764) prior to each trial (RMS, C-weighting, fast response). SPL was measured at the release point of the female (1 m from the speaker). For testing, frogs were placed in a wire release cage at the center of the arena. Trials started once the release cage was remotely opened by pulling a string, and ended once the frog touched the arena wall anywhere in the test arena, or after 20 min had elapsed. An infrared video camera (EverFocus EQ150, EverFocus USA, Duarte, CA) was centrally placed above the arena to monitor the frog's behavior remotely. Data obtained were: (i) "activity", whether or not the frog moved sufficiently to reach the arena wall; (ii) "orientation", the angular deviation relative to the speaker at which the frog touched the wall; and (iii) "approach latency", the time until the frog made contact with the arena wall. Frogs that did not move out of the release cage, or did not reach the arena wall, were scored with a 0 in the "activity" category, and did not contribute to the "orientation" or "approach latency" data set. After testing, we measured snout-vent length (to the nearest 0.1 mm with a caliper), and weight (to the nearest 0.1 g using a digital scale). From these values we calculated body condition using the residuals of a linear regression of length and mass (Schulte-Hostedde et al. 2005). The experimental protocol was approved by the Animal Care and Use Committee of the University of Wisconsin-Milwaukee (protocol no. 07-08#38).

Statistical Analysis

To test which factors affect the activity of frogs (*i.e.*, whether they reach the wall or not), we used logistic regressions implemented in R (R Development Core Team 2008) using the *lme4* package and the function *lmer*. We entered "activity" (coded as categorical variables 0 or 1) as the test variable, and treatment stimulus (Con, Het, N, S), frog SVL and frog body condition as predictor variables in the model. Since each frog was tested with all four treatment stimuli and thus contributed four data points to the analysis, we included trial sequence (coded as continuous variables 1 to 4) as an additional factor, and also added frog ID as a random term in the model. We do not report test statistics for the random frog

ID term, since it was only included to adjust the degrees of freedom. To determine whether the effect of the treatment stimuli were modulated by their order within the trial sequence, we initially also included a treatment x trial sequence interaction term. The interaction term was not significant, and we therefore removed it from the final model. To obtain *p*-values for each term we used the *anova* function to compared the full model against models lacking that particular term.

Next, we were interested in what affected the orientation and speed of movement. A frog touching the arena wall at 30° or 330° relative to a speaker situated at 0° is numerically different, but equivalent in terms of phonotactic precision because they are equally close to the target sound. We therefore transformed the orientation angles into absolute angular deviations from the location of the target sound (*e.g.*, 30° remained 30°, but 330° was transformed to 30°). We calculated test statistics using a mixed model (REML) implemented in JMP 7.0.1 (SAS Institute, Cary, NC, USA), where $F = MS_{num} / MS_{denom}$ and the degrees of freedom are based on an approximation to the distribution of the statistic obtained when the covariance matrix is adjusted using the Kenward-Roger correction. We used a model with orientation or approach latency, respectively, as response variables, and treatment stimulus (Con, Het, N, S), frog SVL and frog body condition as predictor variables. Each frog was tested with all four treatments, and thus contributed up to four data points to the analysis. To account for this we included trial sequence as an additional predictor variable and frog ID as a random term in the model. We do not report test statistics for the random frog ID term, since it was only included to adjust the degrees of freedom. We initially also included a treatment x trial sequence interaction term, but because the interaction was never significant we removed it from the models and only present data from the reduced models. In all cases we confirmed that assumptions for regression analyses are met by visually checking residual plots: in all cases the residual points were randomly dispersed around the horizontal axis.

For visual comparison we also provide an analysis using circular statistics. We tested the null hypothesis that orientation angles were uniformly distributed using Rayleigh tests. If frogs attend to the presented stimuli, orientation angles should not be uniformly distributed, but instead be directed towards the stimulus. Results showed that orientation angles were distributed uniformly, so we did not further test for a specific direction of movement. We used Oriana v. 3.21 (Kovach Computing Services, Anglesey, Wales, UK) to calculate test statistics.

RESULTS

Neither activity (Table 1, Fig 1a) nor orientation (Table 2, Fig. 1b) or approach latency (Table 2, Fig. 1c) were affected by treatment stimulus or female body measures. Overall, we did not find support for the hypothesis that Green Treefrogs use social information to guide their movements during the non-breeding season. Analysis using circular statistics corroborates these results (Fig. 1d): In all four treatments frogs oriented randomly relative to the speaker (in all cases: length of mean vector $r < 0.218$, Rayleigh tests: $Z < 1.238$, $P > 0.29$).

On average, 68.4% of frogs reached the arena wall (Fig. 1a). Activity increased slightly but significantly over the course of the four treatment stimuli each frog was exposed to. Activity was also not constant across individuals; some frogs never reached the wall (*n* = 5, 13%), 16 frogs (42%) reached the wall in one to three out of the four trials they were tested in, and 17 frogs (45%) reached the wall in all four trials. The 16 frogs that only reached the wall in some trials did not show

Table 1. Results of a logistic regression testing the effect of acoustic stimuli, SVL and body condition on frog activity. Activity of Green Treefrogs was not affected by the presented acoustic stimuli

Factor	Chi-square	P
Stimulus	$\chi_3^2 = 0.362$	0.948
SVL	$\chi_1^2 = 1.462$	0.223
Body Condition	$\chi_1^2 = 0.136$	0.712
Trial sequence	$\chi_1^2 = 7.687$	0.007

a predictable pattern in their activity: some only responded in early trials, some only in late ones, and some switched between responding and not responding.

Mean (± SD) latency (across all trials) to reach the wall was 422 + 288 sec, which is about 7 min. (Nota bene: during mate choice trials, mean latencies are 2-3 min, and we generally stop the trial if the frog does not reach a speaker within 5 min). This slow approach latency further underscores that the frogs were not responsive to the playback treatments.

DISCUSSION

Given their highly developed auditory system (Schoffelen et al. 2008), and the robust phonotaxis towards advertisement calls when searching for mates (Ryan 2001, Gerhardt and Huber 2002, Wells 2007), it seems intuitive that anurans might co-opt their hearing capability for use in other behavioral contexts. Yet, studies investigating its use for foraging (Taylor 2001; Höbel et al. 2014) or risk avoidance (*i.e.*, Leary and Razafindratsita 1998; Schwartz et al. 2000; Grafe et al. 2002;

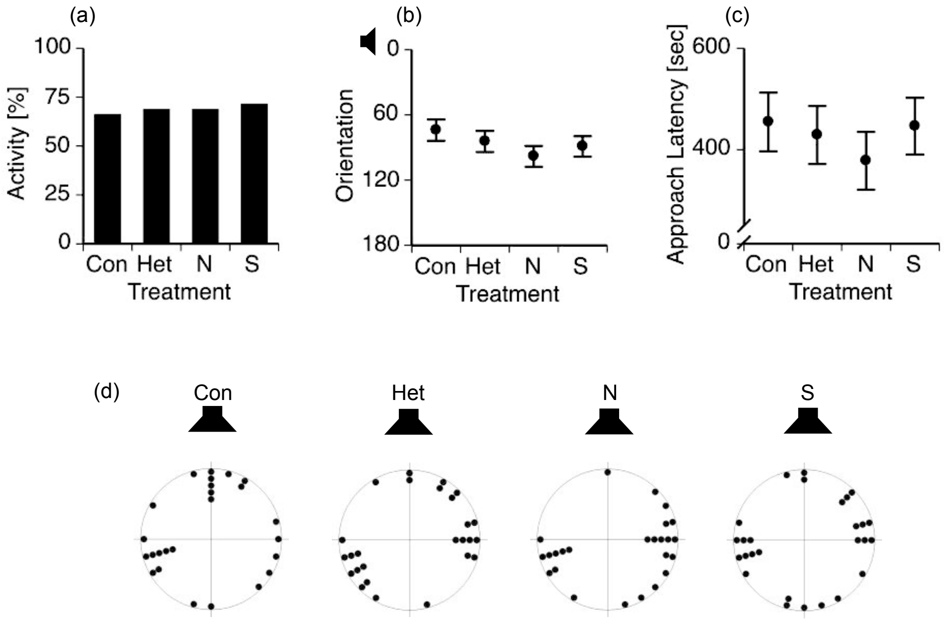

Fig. 1. Responses of Green Treefrogs to presentation of conspecific calls (Con), heterospecific calls (Het), white noise (N) and silence (S). (a) The proportion of frogs that reached the arena wall was similar for the different treatment stimuli. (b) Orientation (angular deviation; least square means ± SE) was not directional towards the speaker presenting treatment stimuli; speaker position at 0 degree. (c) Approach latency was similar across treatments; (d) Polar diagrams showing the locations at which frogs touched the arena wall in relation to the position of the speaker (at 0 degree; top of diagram); each dot represents one frog.

Table 2. Results of Standard Least Squares models testing the effect of acoustic stimuli, SVL and body condition on orientation and approach latency. Neither orientation nor approach latency of Green Treefrogs was affected by the presented acoustic stimuli

Test Variable	Factor	*d.f.*	F	P
Orientation	Stimulus	3,77.94	1.07	0.37
	SVL	1,30.09	0.81	0.37
	Body Condition	1,27.19	0.14	0.71
	Trial sequence	1,79.57	1.01	0.32
Approach latency	Stimulus	3,71.79	0.51	0.68
	SVL	1,28.78	0.003	0.95
	Body Condition	1,27.17	0.55	0.47
	Trial sequence	1,72.94	10.05	0.82

Bernal et al. 2007) are relatively rare, as are studies investigating anuran social information use (but see Lea et al. 2002; Swanson et al. 2007; Buxton et al. 2015). In our experiments female Green Treefrogs did not show phonotaxis to signals associated with the presence of other frogs, and the orientation and speed of their movement was not different from animals randomly moving inside a silent arena.

Examples documenting social information use in anurans and other amphibians are generally restricted to reproduction and the associated chorus environments (Wells 2007). Some anurans use chorus sounds created by calling conspecifics and heterospecifics to find suitable breeding sites (Gerhardt and Klump 1988; Sinsch 1992; Bee 2007; Swanson et al. 2007; Buxton et al. 2015). Even newts, although not vocal themselves, use the calls of frogs and toads to locate breeding sites (Pupin et al. 2007). Some species also seem to use temporal cessation of chorus sounds as indicators of approaching predators (Phelps et al. 2007; Dapper et al. 2011). Interestingly, the vocalizations of predators themselves, which constitute public information available for risk avoidance, are generally ignored by anurans (Schwartz et al. 2000; Bernal et al. 2007; Llusia et al. 2010).

The single example suggesting social information use not associated with breeding choruses comes from midwife toads, which seem to use calls to seek out communal hiding places (Lea et al. 2002). Both communal hiding places and chorus environments represent the more social phases in an anuran's life history, and support the idea that use of social information is associated with increased social interactions (Valone 2007). Further, most species that make use of social information (in the form of chorus sounds) are either explosive breeders or species using unpredictable or ephemeral aquatic habitats (Gerhardt and Klump 1988; Sinsch 1992; Bee 2007, but see Swanson et al. 2007; Pupin et al. 2007), *i.e.*, ecological contexts in which personal sampling may be insufficient to find temporally and spatially unpredictable resources. By contrast, the Green Treefrogs that did not show social information use in our study are prolonged breeders that use a variety of stable environments such as large ponds and swamps for reproduction (*i.e.*, Garton and Brandon 1975; Mitchell and Miller 1991; Gunzburger 2006). This may make it less likely for them to attend to social information to find a breeding site, and even less so outside the breeding context.

Our trials were conducted in a 1-m radius arena, which is standard practice in phonotaxis experiments examining mate choice, *i.e.*, a behavior that occurs at relatively short range and requires high directionality towards the speaker/male (Höbel and Gerhardt 2003). Orientation to social signals during the non-breeding season on the other hand, might occur at relatively long range, and approaching a habitat patch may require lower directionality. It is possible that the lack of response we observed in our trials is an artifact of the differences in scale at which phonotaxis to find a mate during the breeding season compared to finding good habitat outside the breeding season takes place. Repeating the experiment in a larger arena would be required to test this hypothesis.

CONCLUSIONS

The few studies that document behaviors consistent with social information use in anurans are generally conducted with reproductively active frogs during the breeding season (Gerhardt and Klump 1988; Sinsch 1992; Bee 2007; Swanson et al. 2007; Buxton et al. 2015). Our study, on the other hand, used non-reproductive animals, and these did not approach social signals. We propose two non-exclusive hypotheses for this observed difference in phonotaxis behavior between reproductively active and non-gravid frogs. First, attending to sexual and social signals might be restricted to the time periods during which this behavior is most ecologically relevant, *i.e.*, to finding appropriate breeding sites or reproductively active conspecifics during the breeding season. Second, in anurans the hormonal system that regulates reproduction also influences their vocal communication system: changes in hormone levels correlate with changes in calling behavior in males, as well as in how calls are perceived and responded to by females (Aitken and Capranica 1984; Hillery 1984; Arch and Narins 2009; Miranda and Wilsczynski 2009). Thus, in frogs the reproductive state may influence the ability of acoustic signals (sexual or social) to stimulate the auditory system, and audition may be downregulated in frogs that are not reproductively active.

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