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Male Position Relative to Foam Nests Influences Female Mate Choice in the Túngara Frog, *Physalaemus pustulosus*

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ABSTRACT.—Vocalizations are critical advertisement signals used during anuran courtship. In most species, acoustic signals have primacy, but visual cues also have been shown to play an important role in anuran mate attraction. Male Túngara Frogs, *Physalaemus pustulosus*, produce advertisement calls, and males that are successful in attracting a mate build conspicuous white foam nests in which fertilized eggs are deposited. Foam nests persist for several days and on subsequent nights, male frogs are often observed calling adjacent to these foam nests. We tested the hypothesis that females approach the vocalization of a male adjacent to a foam nest preferentially. We conducted choice tests allowing females to choose between two speakers broadcasting a male vocalization—one speaker adjacent to a foam nest and the other speaker lacking a foam nest. Females expressed a significant preference for a speaker with a foam nest when the nest was visible. These results indicate that males may increase their probability of attracting a mate when calling adjacent to a foam nest relative to males located farther from a foam nest.

Vocalizations produced by male anuran amphibians are the dominant signal used for mate advertisement and territory defense (Ryan, 2001; Gerhardt and Huber, 2002). Visual signals also are incorporated into many courtship displays (Hödl and Amézquita, 2001; Amézquita and Hödl, 2004; Taylor et al., 2007; Vasquez and Pfennig, 2007), but these signals tend to play a secondary role to the acoustic signals for most anurans (but see Hirshmann and Hödl, 2006; Grafe and Wanger, 2007). Despite the role as a secondary signal component, visual cues can be an important aspect of many anuran communication systems and can strongly modulate female mate choice behavior (Taylor et al., 2011).

Túngara Frogs, *Physalaemus pustulosus*, are common inhabitants of lowland tropical forests throughout Middle America and breed during the rainy season, May through November. Males congregate and form choruses in shallow pools of water along the forest edges and in disturbed habitats. As is typical for many anurans, the sex ratio on most chorus nights is highly male-biased, and females exhibit mate choice based on acoustic and visual signals (Ryan, 1985; Taylor et al., 2008).

Male Túngara Frogs produce vocalizations that consist of a whine only (simple call) or a whine plus one or more chucks appended to the whine (complex call). Females express a preference for complex calls, and the acoustic communication system in this species has been well studied (Ryan, 1985; Ryan and Rand, 2003). Túngara Frogs also have been shown to retain visual sensitivity at illumination levels typical of nocturnal breeding conditions (Cummings et al., 2008). As in other anuran species, females also use the vocal sac as a visual cue during mate assessment (Rosenthal et al., 2004; Taylor et al., 2007, 2008; Gomez et al., 2009).

During mating, Túngara Frog pairs produce a foam nest in which the fertilized eggs are deposited. The foam nest persists for several days, preventing egg desiccation in the event of a temporary dry-down of the pool (Ryan, 1985). It also may provide some protection against egg predators (Ryan, 1985; Altig and McDiarmid, 2007). The nest is highly reflective, and the bright white coloration is easily visible to a human observer, even under nocturnal conditions.

In the field, we observed that males often call near a foam nest that was produced the previous night. Given that female Túngara Frogs have been shown to use visual cues during courtship (Taylor et al., 2008), we tested the hypothesis that a male calling next to a foam nest increases his probability of attracting a female.

MATERIALS AND METHODS

Collection of Túngara Frog Pairs.—We collected Túngara Frogs from seven sites around Gamboa, Panama (9°7'0"N, 79°42'0"W) between 10 June and 5 July 2008. Pairs found in amplexus were gathered by hand and placed in a plastic bag with a small amount of water. We placed the pairs in a cooler for transport back to the laboratory, where they were left in complete darkness for at least 1 h before testing. This provided time for the frogs' eyes to dark-adapt after collection because headlamps were used to locate them in field.

Collection of Foam Nests.—To ensure we had a constant supply of foam nests that were relatively consistent in size and coloration, we kept a few frog pairs overnight in the laboratory and allowed them to produce foam nests, which we then used in experiments on the following night.

Arena Enclosure.—The testing arena consisted of a dark green, vinyl-like floor material surrounded by a polyvinyl chloride frame supporting foam and acoustic tile walls to dampen reverberations from the acoustic playbacks. We placed a transparent funnel in the center of the arena to restrain females during a habituation period immediately before each playback trial. Equidistant from the funnel, we placed two speakers angled toward the funnel. The speakers were 70 cm apart (Fig. 1). Lighting for the arena was provided by a single GE-brand night light (model 55507). The spectral output of the light source had a broad peak at 512 nm, producing a green color to the human eye (Fig. 2). This spectrum corresponds to light conditions that Túngara Frogs are likely to experience under natural field conditions. The irradiance of light in our arena was 8.57×10^{-10} W/cm². One irradiance measurement from the field under conditions of a new moon was 5.1×10^{-9} W/cm². The down-welling irradiance in our experimental arena was lower than what occurs on many nights in the field, but experimental data have shown that Túngara Frogs retain visual sensitivity at light levels commensurate with those in our arena (Cummings et al., 2008). See Taylor et al. (2008) for detailed discussion regarding arena lighting and relevance to field conditions.

Experiment 1: Foam Nest Visible.—Before the start of each trial, we placed a Petri dish containing 20 mL of spring water and a foam nest in front of one speaker. A Petri dish containing only 20 mL of spring water was placed in front of the other speaker as a control. We placed a female Túngara Frog under the funnel and began broadcasting a digitally synthesized male vocalization (complex call, whine + chuck) antiphonally from each speaker at 82 dB (re. 20 μ Pa). The identical call was broadcast from each speaker to eliminate a female's ability to choose based on distinct call properties. We released the female from the funnel after a minimum 2-min acclimation period to the playbacks and only released her when she was facing the center of the arena (i.e., had visual access to both speakers and foam nest). After each trial, we switched the placement of the foam nest between the left and right speakers to control for position bias.

A choice was scored when the female approached to within 5 cm of a speaker or speaker/foam nest and remained there for 5 sec. If the female did not move for 3 min after being released or did not choose a speaker within 10 min, that trial was discarded from the data set due to a presumed lack of motivation.

Experiment 2: Foam Nest Visually Obstructed.—We conducted a second experiment to ensure that females were using the foam nest as a visual cue and not as an olfactory cue. Again, one speaker had a foam nest in a Petri dish with 20 mL of spring water placed in front of it, whereas the other speaker had only a Petri dish of spring water. We fabricated a visual obstruction using a cylinder of rigid plastic mesh (\approx 10 cm in diameter \times 20 cm in height). Black fabric was wrapped around the mesh cylinder, and the top of the cylinder was left open. We placed the obstructions over the top of the Petri dishes in front of each speaker whether it contained a foam nest or not. This concealed the foam nest from the female's view while presumably allowing her to detect any potential odors that may have diffused through the fabric or dispersed

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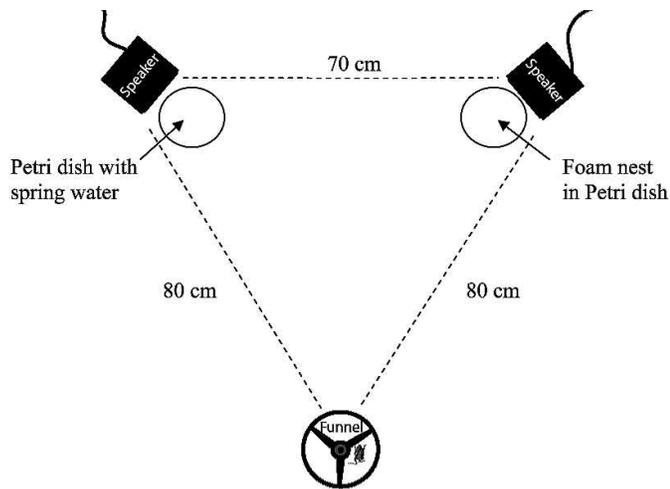


FIG. 1. Diagram of test arena with the female release funnel placed equidistant from the two speakers. Only the front half of the arena is shown in the diagram; the remainder of the arena did not contain any speakers and only provided an area where *Túngara* Frog females were free to move about. The circle in front of the right speaker indicates the position of the foam nest; the position was alternated between trials. The alternative speaker in each trial had a Petri dish with only spring water. In experiment 2, only one speaker contained a foam nest, but both speakers contained identical black fabric baffles to present identical visual cues.

from the open top. Experiment 2 was then carried out following the same methods as for experiment 1.

RESULTS

Experiment 1: Foam Nest Visible.—When we presented females with two identical calls, the females showed a significant preference for the call broadcast from behind a foam nest compared with a call alone (binomial test, 16:8, $P = 0.032$; Fig. 3).

Experiment 2: Foam Nest Visually Obstructed.—When we presented females with identical calls and the foam nest was obscured by black cloth, females failed to show a significant preference for either speaker (binomial test, 12:12, $P = 0.419$; Fig. 3).

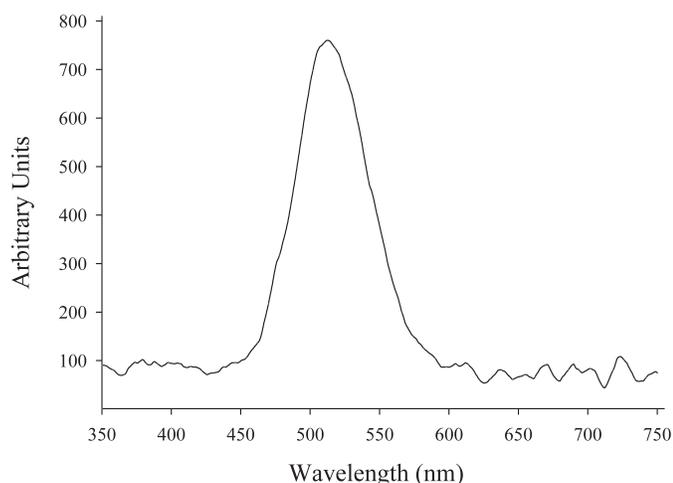


FIG. 2. Spectral output of arena light showing the relative proportion of the spectrum where light energy is emitted. The broad peak occurs at 512 nm and is commensurate with light that is green to the human observer. The y-axis values are arbitrary units because light energy varies with wavelength, and the spectrometer does not calculate light energy relative to wavelength. Measurements were conducted with an Ocean Optics S2000 spectrometer (R400-7 UV/VIS, Ocean Optics, Dunedin, FL).

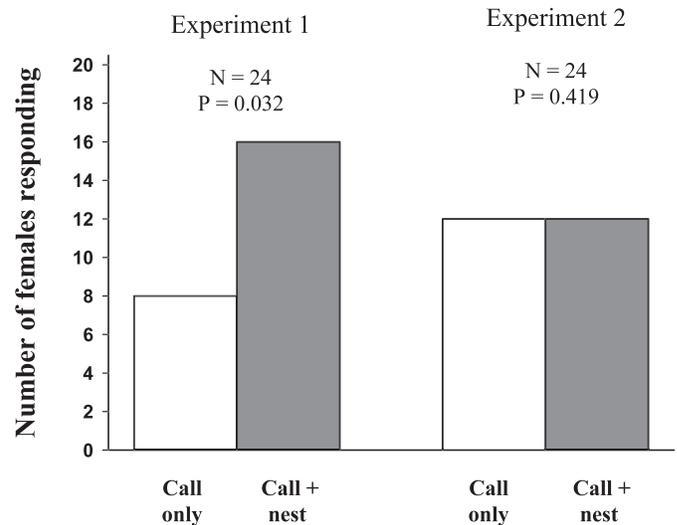


FIG. 3. Responses of female *Túngara* Frogs to visible vs. non-visible foam nest. In experiment 1, the foam nest in front of one speaker was visually accessible to the female in the arena. In experiment 2, the foam nest was visually obscured behind black cloth. In experiment 2, both speakers had the same black mesh cloth (rendering two visually identical targets) in front of the speakers, but only one speaker had the foam nest.

DISCUSSION

Our results demonstrate that all else being equal, males calling adjacent to a foam nest increase their probability of attracting a female. One possible explanation for this behavior is the potential benefit provided by a communal nest. Females in amplexus often approach a pair engaged in nest construction and begin constructing their own nest, attaching it to the first. These communal nests are larger than individual nests and have a lower surface area-to-volume ratio, which may provide additional protection from desiccation or predators (Ryan, 1985), in addition to keeping the eggs in a well-oxygenated environment (Kluge, 1981). Communal nest building, however, is unlikely to explain why females initially approach a male adjacent to a nest (i.e., oviposition site choice). When female *Túngara* Frogs select a male, the pair often leaves the pond for up to several hours before returning to build a nest. Thus, when a female chooses a male near a foam nest, she is unlikely to be choosing that nest as a communal building site at the time of mate choice.

Another possible explanation for attraction to nests is that the nest may render the male's vocal sac more visible. *Túngara* Frogs have been shown to use the vocal sac as a visual cue during mate assessment (Rosenthal et al., 2004; Taylor et al., 2008). This species is cryptically colored against a background of wet soil, typical of their breeding sites. Vocalizing next to a white foam nest may improve contrast and render the male's vocal sac more visible, increasing his attractiveness to potential mates. This explanation is likely, but we did not use a robotic frog (see Taylor et al., 2008) and thus did not test this directly. Interestingly, our data show that even when a vocal sac (calling male) is not visually available, the presence of the foam nest alone is sufficient for increasing the attractiveness of a call.

Two nonmutually exclusive processes may explain the female attraction to foam nests: (1) females may be more likely to approach a male at a foam nest because the nest provides a physical barrier that increases time available for the female to make a mate choice decision or (2) females have a visual bias for increased brightness under very low illumination conditions and are caught in a sensory trap (Hailman and Jaeger, 1976; West-Eberhard, 1984; Christy, 1995).

The first of these explanations is based on video data (Akre, unpubl. data), demonstrating that females who approach a male often physically bump the male, but then swim past him and use the foam nest as a barrier to prevent him from clasping her. Males respond by increasing the complexity of their calls (adding more chucks), and the female will often approach the male a second time, allowing him to clasp her. Thus, the female may be using the foam nest as a physical barrier to increase the time available for mate assessment before being clasped. By calling adjacent to a foam nest, a male may increase the probability that a female will make an initial approach.

Animals can be caught in a “sensory trap” by exhibiting a behavioral response to a particular stimulus that evolved for some other purpose. Hailman and Jaeger (1976) and Jaeger and Hailman (1976) proposed that many species of frogs have an optimum ambient illumination—the light level at which their visual system exhibits the greatest discriminability (i.e., allowing them to forage visually for prey items). Under very dark conditions, such as those experienced by frogs courting in a nighttime forest, many frogs exhibit a photopositive behavior, moving toward areas of brighter illumination (Hailman and Jaeger, 1976). The foam nest may be attractive because it is highly reflective and Túngara Frogs may be exhibiting a photopositive response to this area of brighter reflectance. Thus, their visual system may predispose them to respond to the highly reflective foam nest under nocturnal conditions. Under this sensory trap hypothesis, approaching foam nests may not have an adaptive value for adult frogs but may still provide fitness benefits for males calling adjacent to them.

The failure of females to respond to foam nests when nests are obscured visually (control experiment) suggests that the attraction is visually-mediated. It is possible that the visual obstruction baffles also limited the dispersal of olfactory cues and rendered them unavailable to females. Cloth fabric, however, is more permeable to airborne chemicals than plastic, the top of the baffles around the foam nest were only a few cm taller than the nest, and the fabric on the bottom of the baffles did not fit tightly against the floor of the arena. This design increased the probability that chemical cues would disperse beyond the visual obstruction. Furthermore, when females were released from the restraining funnel, they typically wandered around the arena between the speakers before making a choice. This behavior improved the ability of females to sample chemical cues in a limited dispersal area around the nest. The cloth barriers eliminated the visual cue of the foam nest, but we cannot rule out that olfactory cues were unavailable to females as well. Our design made it likely that olfactory cues were available, however, and suggest that the behavior is visually mediated. Regardless of the mechanism, our data support the hypothesis that males increase their probability of attracting a mate when calling adjacent to a foam nest.

Acoustic signals have primacy in the courtship displays of most anurans (Ryan, 2001; Gerhardt and Huber, 2002); however, recent data have shown that visual cues also play an important role in anuran courtship (Hödl and Amézquita, 2001). In some cases, these visual cues may even modulate female responses to acoustic signals (Richardson et al., 2010; Taylor et al., 2011). In addition, Red-Eyed Treefrogs (*Agalychnis callidryas*) have been shown to communicate using vibrational signals (Caldwell et al., 2010). The data in this study add to the literature demonstrating that signals in modalities outside of vocalizations are important in anuran sexual selection. Thus, a better understanding of anuran sexual selection can come from providing a more complete complement of communication signals to receivers during controlled experiments.

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