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Original Article

Can you hear/see me? Multisensory integration of signals does not always facilitate mate choice

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Females of many species choose mates using multiple sensory modalities. Multimodal noise may arise, however, in dense aggregations of animals communicating via multiple sensory modalities. Some evidence suggests multimodal signals may not always improve receiver decision-making performance. When sensory systems process input from multimodal signal sources, multimodal noise may arise and potentially complicate decision-making due to the demands on cognitive integration tasks. We tested female túngara frog, *Physalaemus* (=*Engystomops*) *pustulosus*, responses to male mating signals in noise from multiple sensory modalities (acoustic and visual). Noise treatments were partitioned into three categories: acoustic, visual, and multimodal. We used natural calls from conspecifics and heterospecifics for acoustic noise. Robotic frogs were employed as either visual signal components (synchronous vocal sac inflation with call) or visual noise (asynchronous vocal sac inflation with call). Females expressed a preference for the typically more attractive call in the presence of unimodal noise. However, during multimodal signal and noise treatments (robofrogs employed with background noise), females failed to express a preference for the typically attractive call in the presence of conspecific chorus noise. We found that social context and temporal synchrony of multimodal signaling components are important for multimodal communication. Our results demonstrate that multimodal signals have the potential to increase the complexity of the sensory scene and reduce the efficacy of female decision making.

Key words: **acoustic noise, mate choice, multimodal perception, sexual selection, túngara frog, visual noise.**

INTRODUCTION

How animals perceive the world around them varies tremendously among species. Each species has a unique sensory physiology underlying perceptual processing. This diversity in perception is, in part, a function of an animal's specific ecology, the receiver's sensory system, and social context (Endler 1992; Ryan and Cummings 2013). Additionally, animals often perceive and communicate simultaneously through multiple sensory modalities (e.g., acoustic and visual) to either choose or attract mates (Partan and Marler 1999; Bradbury and Vehrencamp 2011; Rosenthal 2017). Multimodal signals are commonly assumed to have evolved because they increase information transfer or improve efficacy in noisy environments (Partan and Marler 1999; Rowe 1999; Hebets and Papaj 2005; Partan 2013, 2017). Understanding how receivers perceive and utilize multimodal signals has important consequences for mate choice and can pave the way for testing how receivers perform in naturally complex sensory environments.

It is imperative to consider how receiver sensory processing varies among individuals and to understand its crucial role in multisensory integration and perception. Variation in how a receiver's sensory system is tuned to match specific features of the signal and filter out signals that fall outside the tuning range highlights the importance of individual differences in mating preferences (e.g., Ronald et al. 2012; Ryan and Cummings 2013; Ronald et al. 2018). For instance, a receiver with higher auditory sensitivity for certain frequencies will have a lower auditory threshold for those frequencies and thus may have a greater preference for songs or calls with peak amplitudes at those frequencies (e.g., Ryan et al. 1992; Gerhardt 2005; Kostarakos et al. 2008). Receiver sensory systems also dictate how multiple signal components are integrated into coherent

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percepts. Multimodal signals might not sum linearly, as signal components from separate modalities might be processed by receivers independently or integrated into a single multimodal percept, generating a different sensory experience compared to the experience resulting from each individual component alone (Stein 2012; Taylor and Ryan 2013; Rosenthal 2017). This phenomenon is seen in the McGurk effect in human speech perception, whereby an auditory component is integrated with a visual component, forming a novel percept of the auditory component (McGurk and Macdonald 1976). For speech perception, temporal synchronization of visual and acoustic components is often necessary for multisensory integration (McGurk and Macdonald 1976; Ghazanfar et al. 2005), and temporal asynchrony can drastically reduce the attractiveness of a signal (e.g., Taylor et al. 2011, 2017).

In complex environments cluttered with signals and noise from multiple modalities, receivers must not only integrate components of a multimodal signal but also accurately assign the separate multimodal components to individual signalers. Noise is commonly thought of as extraneous acoustic stimuli, but noise can affect any modality and generate cross-modal interference (Gorea and Sagi 2001; Ord et al. 2007; Halfwerk and Slabbekoorn 2015; Halfwerk et al. 2016). We define noise as excess sensory stimuli (e.g., extraneous sound or extraneous light) that disrupt information transfer between signalers and receivers. Thus, while multimodal signals can increase signal detectability in some noisy environments, processing of these signals by receivers may be complicated by multimodal noise. This complication is especially true for animals like anurans that form dense aggregations, where both conspecific and heterospecific signals are produced in abundance by males to attract females (Gerhardt and Huber 2002; Wollerman and Wiley 2002). A substantial body of work has shown that many anurans employ both auditory and visual signal components for communication (e.g., Taylor et al. 2007, 2008; Grafe et al. 2012; Preininger et al. 2013; Starnberger et al. 2014; Laird et al. 2016; Zhao et al. 2021; Zhu et al. 2021) and are thus excellent models for understanding how receivers perceive multimodal displays in complex signaling environments (Bee 2015).

The túngara frog, *Physalaemus* (=*Engystomops*) *pustulosus*, is found from southern Mexico to northern South America. Males congregate in ephemeral ponds and puddles and produce calls (typically consisting of a whine and one to three chuck notes) to advertise for mates. While calling, males inflate a vocal sac in their throat. The vocal sac inflation is biomechanically linked to call production, thus males cannot naturally alter this timing. Some frog species also add a visual component to their sexual display (e.g., foot flagging) that is produced independently of the call (Grafe et al. 2012; Preininger et al. 2013). The anuran vocal sac reduces energetic expenditure during calling and evolved in that context (Pauly et al. 2006). Several species, including the túngara frog, have co-opted the movement of the vocal sac as part of their signaling system (Taylor et al. 2008; Starnberger et al. 2014; Laird et al. 2016). This likely occurred as a preexisting bias by the frogs' visual system to motion (Lettvin et al. 1959; Ryan and Cummings 2013).

The túngara frogs is an excellent candidate for studying multimodal signaling and noise; previous studies have documented multimodal interactions between male advertisement calls, vocal sac inflations, and female mate choice (e.g., Taylor et al. 2008, 2011; Taylor and Ryan 2013; Taylor et al. 2017, James et al. 2021). Vocal sac inflations, combined with advertisement calls, make túngara frog signals more attractive to females (Taylor et al. 2008). Females attend to the timing of the vocal sac inflation and respond preferentially to a vocal sac inflating synchronously with a call (Taylor et al. 2008). However, if inflation occurs out of phase (asynchronously), such that inflation lags the call, females avoid this asynchronous multimodal stimulus in favor of just a call (e.g., Taylor et al. 2011). Conversely, females will respond positively to a delayed vocal sac inflation if the vocal sac inflation is sandwiched between the whine and chuck notes (Taylor and Ryan 2013).

Social context is crucial for determining female preferences in túngara frogs. In a unimodal context, mate choice preferences for a typically attractive and unattractive call can shift solely with the addition of a third, inferior male call (Lea and Ryan 2015). Thus, females do not assess calls in a rational manner. When females are given the choice between an attractive and unattractive call in quiet conditions, the addition of a robotic túngara frog (robofrog) inflating synchronously with an unattractive call does not make that call more attractive. When females are presented with the same stimulus pair in the presence of background noise, females choose the unattractive call with the robofrog about as often as the attractive call lacking the robofrog. Interestingly, this occurs with background noise levels that are not sufficient to mask the call stimuli (Taylor et al. 2021). But it is still unknown how female preferences change in complex conditions, where females are evaluating visual cues and acoustic signals from males amidst naturalistic background noise (both acoustic and visual) from other conspecifics and heterospecifics.

In natural choruses, multiple males often call in close proximity. The acoustic and visual components are favored by female receivers when they perceive them as a coherent unit and thus act as a multimodal signal. Natural choruses are physically heterogeneous environments; vegetation, logs, natural soil berms, and intense chorus noise may combine to obscure parts of the multimodal display, complicating perceptual binding of these components by female receivers. These disrupted components have the potential to create both visual and acoustic noise when females are evaluating potential mates. Thus, we cannot fully understand the evolution of multimodal communication between signalers and receivers by studying their interactions in the absence of noise (Wiley 2015).

For the first time, we investigated how the vocal sac inflations of other male túngara frogs surrounding the signaler can induce visual noise for female mate choice. Similar to conspecific background choruses, this visual noise has the potential to complicate signal processing by receivers. We also incorporated acoustic noise from heterospecifics and conspecifics with the visual noise to reflect a more natural sensory environment. In this study, we ask: (1) whether females can express known preferences in the presence of acoustic and visual noise, (2) whether the type of acoustic noise (heterospecific or conspecific) changes female response to preferred calls, (3) if multimodal noise disrupts known female preferences, and (4) if a multimodal signal can improve acoustic discrimination in the presence of noise. From previous research on female mate choice in túngara frogs, we predicted that visual noise would disrupt female mate choice and that similar results would follow from multimodal noise using either heterospecific or conspecific calls as acoustic noise (Table 1).

MATERIALS AND METHODS

Field collection

We conducted all experiments at the Smithsonian Tropical Research Institute (STRI) in Gamboa, Republic of Panama, between 4 June and 7 August 2019. We collected female and male túngara frogs as

Table 1

Predictions of significant effects of noise from two modalities (acoustic and visual) on the proportion of females choosing the attractive stimulus (In quiet conditions = 75%, Ryan and Rand 2003; Coss et al. 2021). These predictions are derived from previous research (Taylor et al. 2011; Coss et al. 2021; Taylor et al. 2021) on the influence of chorus noise and multimodal signals on female mate choice in túngara frogs. In the experimental design of the treatments, synchronous vs. asynchronous visual components refer to the three robofrogs and whether the two in front of the stimuli speakers inflate synchronously (multimodal signals) or asynchronously (visual noise) with the nearest acoustic stimulus. The middle robofrog always acts as visual noise. Heterospecific and conspecific refer to the type of acoustic noise broadcast from the two corner noise speakers.

	Type of Acoustic Noise		
	None	Heterospecific	Conspecific
Type of Visual Noise	Prediction: The proportion of females choosing attractive stimulus should		
Synchronous (Multimodal Signal and Distractor Robofrog)	Not change	Not Change	Not Change
Asynchronous	Decrease	Decrease	Decrease

amplectant pairs nightly between 1930 and 2100 h. We brought the pairs to our laboratory at STRI facilities and placed them in total darkness in a cooler for at least 1 h before testing. This hour allowed their eyes to dark adapt after collection with flashlights (Fain et al. 2001; Taylor et al. 2008). On a typical night, we collected 6–14 pairs of frogs with roughly 70% of those females responding in a phonotaxis trial. Sample size for all treatments in this study was n=32; a total of 288 frogs texted in the nine treatments. We toe-clipped (please see *Ethical Note* below) and measured mass and snout-vent length (SVL) for each frog before returning pairs to their respective breeding pools on the same night of collection.

Experimental design

We tested all females from 2200 to 0330 h on the same night we collected them. The temperature of the sound attenuation chamber (Acoustic System, ETS-Lindgren, Austin, TX, USA), where we tested the frogs, was kept ca. 27°C, similar to nighttime temperatures in the field. We illuminated this chamber with a GE nightlight (ca. 5.8 x 10^{-10} W/cm^2, model no. 55507; Fairfield, CT, USA) to resemble a nocturnal light level within the range of natural light experienced by túngara frogs (Taylor et al. 2008). For each trial, we placed a female under an acoustically and visually transparent plastic funnel (ca. 10 cm diameter) at the center of this chamber. The plastic funnel had a cutout in the front where we put black mesh, so that females could evaluate the visual cues while under the funnel. The funnel initially held the females equidistant at 80 cm from two speakers (Mirage Nanosat Black, Klipsch Audio, Indianapolis, IN, USA) separated in azimuth by 60°. In all experiments, we antiphonally broadcast amplified (NAD C-316BEE, Pickering, Ontario, Canada) stimuli using Adobe Audition 2.0. The stimuli were natural calls, "Od" and "Sc," with a known preference function (75% of females prefer Od to Sc; Ryan and Rand 2003; Coss et al. 2021). To avoid confounding stimulus call property differences in background noise, we chose to use a single call pair. In this study, we were not testing general female preference functions. Instead, we were interested in testing the influence of various noise types (visual and acoustic) on the ability of females to express their mating preference. We adjusted the stimuli so that their peak amplitudes measured 82 dB SPL (fast, C weighting, re 20 μPa) from the female's release point using a Larson Davis 831 Class 1 SPL meter (Larson Davis, Depew, NY, USA). All sound files played the stimuli on a 3 s loop with an inter-stimulus interval of 1.1 s. Between trials, we alternated the stimuli broadcast from the speakers to avoid potential side bias. The 1.1 s interval provided enough time to add an asynchronized robofrog vocal sac inflation in visual noise treatments (see below).

For each trial, we separated a female from her male and placed her under the funnel. We then played the treatment files for a 2-min acclimation period. Females under the funnel could see and hear the stimuli during this time. We then released a female by raising the funnel with a pulley system outside the chamber. If the female entered a 5-cm radius around a speaker and remained there for at least 3 s, we scored her as making a choice. Alternatively, if the female failed to leave the initial funnel zone within 2 min or wandered around the chamber for 10 min without making a choice, we removed her from the chamber and retested her once more later that evening. If a female failed to make a choice on her second attempt, we did not include her in the dataset. We also recorded the female's latency to choose and noted her path to the chosen stimulus. All trials were video recorded using an infrared video camera mounted on the ceiling of the chamber directly above the funnel zone and EthoVision (Noldus) software. Following these general procedures, we conducted a series of experiments (Table 2) to test female responses in the presence of unimodal noise (acoustic- or visual-only) compared to multimodal noise. Given that female túngara frog mate preferences are consistent (Ryan et al. 2019a), female responses in phonotaxis experiments provide a robust measure for testing how background noise from multiple modalities affects female perception of males.

Acoustic noise trials

Previous research demonstrated that higher densities (duty cycles) of chorus noise, reflective of nights with bustling choruses, can impair female ability to discriminate between males, while lower densities of chorus noise have no significant effects on discrimination (Coss et al. 2021). These results revealed the chorus density threshold at which females can no longer distinguish males in heterospecific noise: gladiator (*Hypsiboas rosenbergi*) and hourglass (*Dendropsophus ebraccatus*) tree frogs, and conspecific acoustic noise. In this study, we compared the acoustic, visual, and multimodal noise treatments to the control to examine the impact of increasing noise complexity. As a summary of how the acoustic noise treatments were conducted in our previous study, we broadcast either low-density conspecific or mid-density heterospecific noise, corresponding to nights with low- and mid-level calling activity (Coss et al. 2021), from two speakers mounted on the back wall (behind the speakers playing the acoustic stimuli) in each of the corners (125 cm above ground; 210 cm from the female release point; Fig. 1A). Mounting these two noise-broadcasting speakers above the floor of the chamber and on the corners generated an even, chorus-like distribution of noise within the chamber. As with the acoustic stimuli, peak amplitudes of the acoustic noise (both conspecific and heterospecific) were calibrated to 82 dB SPL from the funnel zone. This noise level is typical at frog ponds.

Table 2

Treatment summary detailing the type of noise (acoustic only, visual only, or multimodal) and general setup for each experiment. Solid black line separates experiments from Coss et al. 2021 study (top) to experiments in this study (bottom). The control was used for both studies and was conducted in the 2019 season with the rest of the experiments. In all treatments, the same stimuli, Od and Sc (Ryan and Rand 2003), were used. Treatments with visual components (three robofrogs: two in front of speakers and one in between speakers) are named as "synchronous" or "asynchronous" to designate whether the two robofrogs associated with the acoustic stimuli inflated synchronously (multimodal signal) or asynchronously (visual noise) with those stimuli.

Treatment	Noise Type	Description
Control	None	No noise (Coss et al. 2021)
Heterospecific	Acoustic	Mid density of heterospecific noise (Coss et al. 2021)
Conspecific	Acoustic	Low density of conspecific noise (Coss et al.2021)
Synchronous	Visual	Two robofrogs in front of speakers inflate synchronously with their respective stimulus, functioning as multimodal signals; one robofrog in between stimuli speakers functions as visual noise
Asynchronous	Visual	All three robofrogs inflate asynchronously with stimuli, functioning as visual noise
Synchronous Heterospecific	Multimodal	Synchronous and heterospecific treatments combined
Asynchronous Heterospecific	Multimodal	Asynchronous and heterospecific treatments combined
Synchronous Conspecific	Multimodal	Synchronous and conspecific treatments combined
Asynchronous Conspecific	Multimodal	Asynchronous and conspecific treatments combined

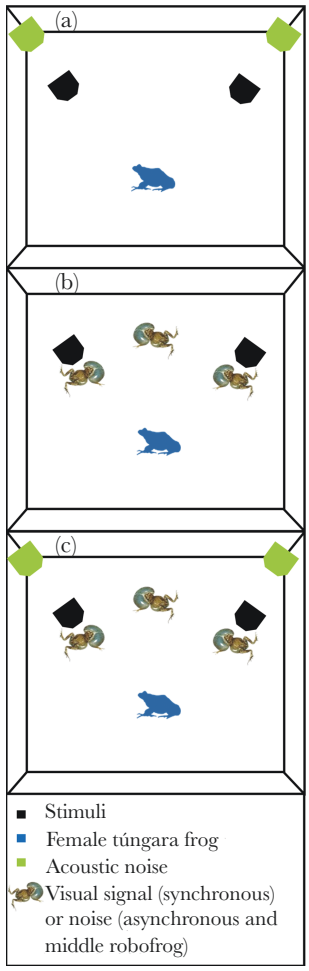

Figure 1

Phonotaxis chamber setup for noise treatments. Chamber is not to scale. (A) Acoustic-only noise includes two wall-mounted speakers broadcasting either mid-density heterospecific or low-density conspecific, depending on treatment (Coss et al. 2021). (B) Visual-only noise includes three robofrogs, two of which inflate either synchronously or asynchronously (depending on the treatment) with the closest acoustic stimulus to either simulate a multimodal signal (synchronous) or extraneous visual noise (asynchronous). The middle robofrog always functions as visual noise. (C) Multimodal noise treatments include the two wall-mounted acoustic noise speakers, the middle/distractor robofrog, and the two robofrogs, functioning as either multimodal signals (synchronous) or noise (asynchronous), as in the visual-only treatments. The same general setup was used for all four combinations of multimodal treatments.

Visual signals/Noise trials

To simulate a visually noisy environment, we placed three robotic túngara frogs (robofrogs) with inflatable vocal sacs in the chamber (one in front of each stimuli speaker and one in between these speakers; Fig. 1B). Robofrog models were designed and 3-D printed by Savi Made (Windsor, Ontario, Canada). We made the vocal sacs using silicone rubber (Dragon Skin™ 10 Medium) and solvent (NOVOCS™ Gloss; Smooth-On, Macungie, PA, USA). We added a pastel purple dye to the mixture to replicate the color of a túngara vocal sac. After casting the molds, we placed a thin line of white silicone pigment on front of inflated vocal sacs (10 cc) to resemble the white stripes present on the túngara vocal sac. We attached the opening of the mold to silicone tubing (Tygon® SPT 3350; United States Plastic Corporation®, Lima, OH, USA) using a silicone rubber adhesive (Sil-Poxy®; Smooth-On, Macungie, PA, USA). This tubing was connected to one of three pneumatic pumps located outside the test chamber. These pumps were controlled by a computer, allowing the robofrogs to be triggered to inflate and deflate either synchronously or asynchronously with the acoustic stimuli (see Taylor et al. 2008 for additional details). The middle robofrog (not associated with a speaker) inflated during the 1.1 s silent gaps between the acoustic stimuli and completely deflated before the onset of the next call at either of the two stimulus speakers, thereby acting as visual noise. In one treatment, the robofrogs associated with the stimulus speakers inflated synchronously with their respective acoustic stimulus (generating a multimodal stimulus). In the second treatment, the robofrogs inflated asynchronously with the acoustic stimuli, where inflations began 130 ms after the closest acoustic stimulus ended, providing additional visual noise. Thus, the robofrog inflation overlapped some background noise but was fully asynchronous with the call at its stimulus speaker. This created visual noise at the stimulus speaker. In both treatments, the acoustic stimuli and robofrog combinations on the left and right alternated, such that there was no overlap between them. The asynchronous visual noise treatment was designed to mimic a complex chorus, where a female may be able to see a male's vocal sac inflate but not detect his call due to acoustic masking. Males in nature are constrained to inflate their vocal sac synchronously with their call and females do not respond to the inflating vocal sac unaccompanied by a call (Taylor et al. 2008). Thus, we considered any vocal

sac inflation that was not in-phase with a call as visual noise. Also, because females preferentially respond to a synchronous inflating vocal sac, we considered any robofrog inflating synchronously with the call at a speaker to be a multimodal signal.

Multimodal noise trials

We merged acoustic and visual noise to make several combinations of multimodal noise treatments (Table 2; Fig. 1C). These treatments contained either the mid-density heterospecific or low-density conspecific acoustic noise (Coss et al. 2021). Visually, treatments had: a) synchronously inflating robofrogs at the stimulus speakers, with only the independent, middle robofrog acting as visual noise, or b) all three robofrogs inflating out-of-phase with the calls at the two stimulus speakers. In the synchronous multimodal noise treatments, like in the synchronous visual treatments, the robofrogs on the right and left were synced to their respective stimuli with an extraneous middle robofrog (visual noise) not synced to either the stimuli or the acoustic noise. Multimodal noise treatments were primarily used to examine if the integration of acoustic and visual noise alters female perception of the stimuli or cognitively overwhelms females. Again, we consider synchronous inflation of the vocal sac as a signal and asynchronous inflation as noise.

Statistical analyses

We tested for differences in female phonotactic preferences between the control and noise treatments using a binomial distribution (SISA binomial calculator; Uitenbroek 1997). We report significance levels for preferences as mid-*P*-values, previously recommended for use in categorical data for smoothing radical changes in *P*-value generated by discrete data (Agresti 2001; Hwang and Yang 2001). For all statistical analyses comparing preferences in experimental treatments to the control, expected values were set to a 0.75 probability value. We chose this value based on previous experiments confirming a consistent 75% preference for the Od over Sc call (Ryan and Rand 2003; Coss et al. 2021). After transforming the data with a natural log function to satisfy assumptions of normality and homogeneity of variance, we performed an Analysis of Variance (ANOVA) on the latency data from this study. All statistical analyses on latency data ($\alpha = 0.05$) were conducted in R software (R Core Team 2018).

Ethical note

All experimental procedures followed ABS ethical guidelines to minimize the impact on animal welfare (Buchanan 2012). Experiments were conducted with approval by IACUC protocols from Salisbury University and the Smithsonian Tropical Research Institute (IACUC: SU-0052 and STRI 2018-0411-2021). The Ministry of the Environment of Panama (MiAmbiente) approved and issued collecting permits (ANAM: SE/A-44-18 and SE/A40-19). After experimentation, we toe-clipped each female that made a choice along with their respective male partners to ensure that females were not retested after recaptures on subsequent collecting nights. For toe clipping, we followed regulations from the American Society of Ichthyologists and Herpetologists (Beaupre et al. 2004). For continued efforts towards monitoring the population genetics of this species, we preserved all toe clips in ethanol for genetic analysis. Our long-term experience with túngara frogs and toe clipping suggests this process does not negatively affect their survivability or reproductive behaviors. We also frequently recapture both sexes weeks or even months after initial capture.

RESULTS

Behavioral experiments

Acoustic noise

In the control, females responded to the attractive call 75% of the time (24 attractive: 8 unattractive, two-tailed binomial test: $P = 0.919$; Coss et al. 2021; Fig. 2). Compared to this control, there were no significant differences in the strength of female preference for the typically more attractive call when the test was conducted in the presence of either heterospecific noise (22:10, two-tailed binomial test: $P = 0.361$; Coss et al. 2021; Fig. 2) or conspecific noise (27:5, two-tailed binomial test: $P = 0.265$; Coss et al. 2021; Fig. 2).

Visual signals/Noise

When robofrogs were added as a visual component, there were no significant differences from expected preference for the more attractive of the two calls. This finding was true when the robofrogs acted as a visual signal (e.g., left/right robofrogs inflating synchronously with calls) (24:8, two-tailed binomial test: $P = 0.919$; Fig. 2) and noise (e.g., left/right robofrogs inflating asynchronously with calls) (24:8, two-tailed binomial test: $P = 0.919$; Fig. 2).

Multimodal noise

When we combined visual noise and mid-density heterospecific chorus noise, we still did not find a significant difference in either synchronous, multimodal signal (26:6, two-tailed binomial test: $P = 0.479$; Fig. 2) or asynchronous, visual noise (19:13, two-tailed binomial test: $P = 0.052$; Fig. 2) multimodal treatments, although the latter experiment suggests a trend towards that effect. However, when we added visual noise with the low-density conspecific chorus noise, the proportion of females choosing the typically more attractive call was significantly reduced for both synchronous, multimodal signal (17:15, two-tailed binomial test: $P = 0.005$; Fig. 2) and asynchronous, visual noise (18:14, two-tailed binomial test: $P = 0.018$; Fig. 2) multimodal treatments. We note that the results of this latter experiment are near identical to the heterospecific asynchronous visual noise experiment reported above.

Latencies

We did not find significant differences in the latencies to choose a speaker by females across the different treatments. From our previous study, latencies were not significantly different for mid heterospecific and low conspecific acoustic noise when compared to the control (Coss et al. 2021). Likewise, we did not find any significant differences in latency between the treatments (visual and multimodal noise) and control (ANOVA: $F_{6, 217} = 1.25$, $P = 0.284$) in this study.

DISCUSSION

Multimodal communication has been studied in a variety of taxa for over two decades (e.g., shrimp: Hughes 1996; birds: spiders: Hebets 2005; Elias et al. 2006; frogs: Taylor et al. 2007; mammals: Rundus et al. 2007; Dalziell et al. 2013; Preininger et al. 2013; Ullrich et al. 2016; Grafe and Tony 2017), but we know very little about how noise, especially from multiple modalities, influences mate choice. In this study, we examined how these sources of noise can alter female túngara frog responses to a known mating preference.

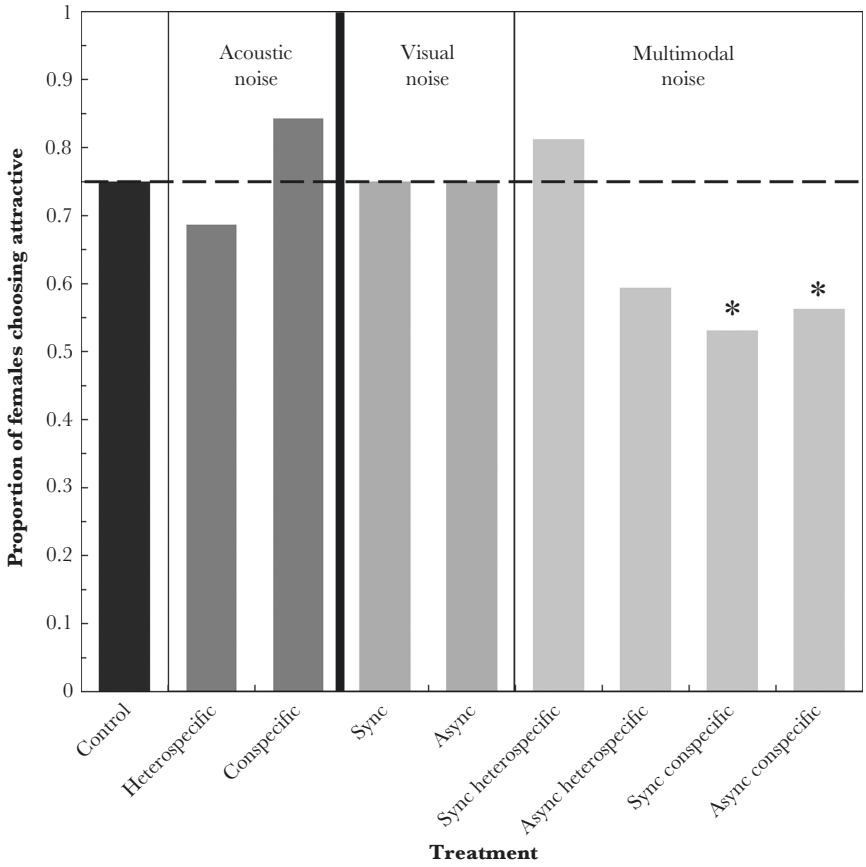

Figure 2
Female túngara frog responses (n=32 for the control and each noise treatment) to stimuli in control (quiet) and noise treatments. Solid black line separates experiments from Coss et al. 2021 study (left) to experiments in this study (right). Values indicate the proportion of females that chose the attractive stimulus for each treatment. The dashed line denotes the expected proportion of females choosing the attractive stimulus (75%) based on the quiet control treatment. Asterisks indicate significant differences from the control when $P < 0.05$.

In the unimodal noise treatments, neither acoustic nor visual noise alone significantly reduced female preferences for an attractive call. This was true for both conspecific and heterospecific acoustic noise, demonstrating that the background acoustic noise levels were insufficient for masking acoustic signal detection. Even though the background acoustic noise was broadcast at the same amplitude, the spatial separation and silent gaps in the noise calls prevented these calls from acoustically masking the stimulus calls (Vélez and Bee 2010; Ward et al. 2013).

Interestingly, in asynchronous visual noise, females still chose the more attractive male call 75% of the time, seemingly disregarding the visual noise altogether. Taylor et al. (2011) demonstrated that when the vocal sac inflates asynchronously after the end of the call, females will choose the alternative stimulus lacking the visual component. The avoidance of the asynchronous vocal sac in that study, however, occurred when alternative was the same call with no moving visual component (Taylor et al. 2011). In the current study, the asynchronous visual noise was associated with both calls and did not disrupt the females' ability to express a preference for the attractive call. Thus, females were able to ignore the visual noise occurring equally at both calls. When the vocal sacs inflated synchronously with the call, generating a multimodal signal (and only the center robofrog unassociated with the call), females also maintained preference for the attractive call. In this scenario, both speakers were displaying a multimodal signal, as occurs in nature, so the maintenance of preference was unsurprising. Even in the synchronous treatment, the middle, distractor robofrog had little effect.

Unlike the unimodal noise treatments (acoustic or visual), females presented with certain types of multimodal noise failed to express a significant preference for the attractive call. Neither the synchronous nor asynchronous heterospecific multimodal noise treatments significantly reduced the preference. Females in the asynchronous heterospecific treatment performed as well as females in the quiet control. Though not statistically significant, there did appear to be some effect of the asynchronous heterospecific noise treatment with 40.6% of females choosing the unattractive stimulus. This suggests that females may have started to reach a level of sensory complexity that was beginning to interfere with their ability to discriminate among the calls. The strongest influence of multimodal noise occurred when the visual noise was combined with the conspecific background chorus; in the asynchronous conspecific multimodal noise treatments, female responses to the two call types were significantly different from random. This finding suggests that even on nights with low densities of conspecific chorus noise, female responses to attractive calls are influenced when visually evaluating multiple calling males. In the synchronous treatments, the robofrogs inflated in-phase with the calls, stimulating the multimodal signal of a calling male. Here, in the presence of conspecific calls, females

again failed to express a significant preference for the attractive call. In this case, the multimodal signals did not improve call discrimination; our findings suggest that this level of signal processing may have cognitively overwhelmed the females' ability to discriminate between attractive and unattractive calls.

While the anuran vocal sac evolved to improve male calling efficiency, it can also serve as an important visual cue for inter- and intraspecific communication (Pauly et al. 2006; Preininger et al. 2013; Starnberger et al. 2014). In some contexts, with multiple males calling and inflating their vocal sacs, the vocal sac inflations occurring simultaneously with vocalizations can aid in the localization of males amidst acoustic background noise (Taylor and Ryan 2013; Taylor et al. 2021). However, as the sensory scene becomes more complex, components of complex signals have the potential to create multisensory noise, potentially interfering with signal detection and decision-making (Taylor et al. 2021).

The background acoustic noise levels alone were insufficient to mask detection of the attractive call. In the absence of background acoustic noise, visual cues did not alter preference for attractive calls. Only in the presence of multimodal noise were females unable to accurately distinguish the attractive from the unattractive call. Our results suggest that females do not merely switch reliance on sensory channels (e.g., acoustic to visual) amidst acoustic noise. This conflicts with other findings suggesting that multimodal signals increase signal efficacy in acoustically noisy environments, such as the case of the Bornean foot-flagging frog (*Staurois parvus*) (e.g., Grafe and Tony 2017). The type of acoustic noise may explain this difference; acoustic noise in the foot-flagging frog study was from a stream, whereas we broadcast calls from heterospecifics and conspecifics. Processing multimodal signals amidst heterospecifics and especially conspecifics is likely a more difficult perceptual task than doing so in the presence of constant stream noise, as females must attend to the advertisement calls and attempt to distinguish species identity and signal attractiveness. In certain social contexts, where assigning multiple acoustic components to their correct source is difficult, the relatively large vocal sac of the male túngara frog can improve signal detectability by females (Taylor and Ryan 2013). In the presence of chorus noise, however, this vocal sac can also complicate the female's discrimination task. Our findings highlight the importance of accounting for multimodal displays and natural acoustic noise for studies of sexual selection.

Synchronization and sequence of multimodal signal components can significantly influence signal function and perception yet is an understudied topic of animal communication (Partan 2013; Uy and Safran 2013; Hogan and Stoddard 2018). For example, researchers have only recently discovered the signaling potential of the aerial courtship dive in male broad-tailed hummingbirds (*Selasphorus platycercus*), where changes in elaborate coloration from the speed and trajectory of the dive are synchronized with song components (e.g., Hogan and Stoddard 2018). How the synchrony of this display influences female perception is still unclear, but, in general, female perception and subsequent receptivity to multimodal signals can change significantly depending on the temporal synchrony of signaling components. In the brush-legged wolf spider (*Schizocosa ocreata*), females are significantly less receptive to multimodal signaling components (visual and vibratory) when they are asynchronous compared to when they are synchronous (e.g., Kozak and Uetz 2016). In túngara frogs, females respond less to asynchronous multimodal signals if the vocal sac inflates after the end of the call but will respond similarly to an acoustic-only signal if it inflates before the beginning of the call, demonstrating not only the importance of synchrony but also sequence of individual signal components (e.g., Taylor et al. 2017). In the presence of multimodal noise, a female's perception of one male's display may be altered by calls and vocal sac movements from nearby frogs.

The structure of acoustic noise (e.g., its spectral and temporal properties) also matters for signal processing in anurans (e.g., Lee et al. 2017; Coss et al. 2021). Noise that utilizes properties of conspecific or heterospecific calls, for example, may elicit greater selective attention than white noise that lacks the structure of conspecific or heterospecific calls (Fan et al. 2019). In the presence of conspecific acoustic noise, accurately assigning relevant sounds to their source is expected to be especially difficult (Nityananda and Bee 2011). This could explain why we found the proportion of females choosing the attractive stimulus to be significantly reduced in our multimodal treatments with conspecific noise, even when vocal sacs inflate synchronously with their respective stimuli, forming multimodal signals that should improve discrimination. Conversely, females may simply be cognitively overwhelmed with the added information from both modalities. That is, heterospecific calls are likely easier to filter than conspecific calls. In the presence of conspecific acoustic noise, females may reach the point where they can no longer process all the relevant information, and the cognitive sensory load diminishes their ability to distinguish between two callers of differing attractiveness.

CONCLUSION

We have shown that the type of acoustic noise used to study female perception of multimodal displays can lead to interesting differences in the outcome of female mate choice. Our study attempts to mimic some of the natural conditions by employing natural calls and similar chorus noise densities experienced by túngara frogs at our field sites (Coss et al. 2021). To better understand the perception and evolution of multimodal displays, it is important that more studies explore how signals are evaluated in noisy (i.e., naturalistic) conditions.

We cannot always predict how animals will respond in cognitive tasks. Mate choice decisions are especially unpredictable when multimodal displays are processed nonlinearly (Lea and Ryan 2015) and when these mating decisions transpire in complex sensory environments, such as is the case for female túngara frogs (Ryan et al. 2019b). In this study, we have further demonstrated this point, elaborated on the importance of social context in mate choice, and found a point where we see behavioral shifts in cognitive performance and perception of multimodal displays in the presence of multimodal noise. We have integrated findings from previous research on multimodal communication in the túngara frog while adding novel elements to advance our understanding of female mate choice in natural breeding conditions. With our growing knowledge of multimodal perception in complex sensory environments, it is becoming increasingly apparent that noise matters in the evolution of communication (Wiley 2015).

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Data accessibility: Analyses reported in this article can be reproduced using the data provided by Coss et al. (2022).

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