

RESEARCH ARTICLE

Complex sensory environments alter mate choice outcomes

Ryan C. Taylor^{1,2,*}, Kyle O. Wilhite^{1,3}, Rosalind J. Ludovici¹, Kelsey M. Mitchell¹, Wouter Halfwerk⁴, Rachel A. Page², Michael J. Ryan^{2,3} and Kimberly L. Hunter¹

ABSTRACT

Noise is a common problem in animal communication. We know little, however, about how animals communicate in the presence of noise using multimodal signals. Multimodal signals are hypothesised to be favoured by evolution because they increase the efficacy of detection and discrimination in noisy environments. We tested the hypothesis that female túngara frogs' responses to attractive male advertisement calls are improved in noise when a visual signal component is added to the available choices. We tested this at two levels of decision complexity (two and three choices). In a two-choice test, the presence of noise did not reduce female preferences for attractive calls. The visual component of a calling male, associated with an unattractive call, also did not reduce preference for attractive calls in the absence of noise. In the presence of noise, however, females were more likely to choose an unattractive call coupled with the visual component. In three-choice tests, the presence of noise alone reduced female responses to attractive calls and this was not strongly affected by the presence or absence of visual components. The responses in these experiments fail to support the multimodal signal efficacy hypothesis. Instead, the data suggest that audio-visual perception and cognitive processing, related to mate choice decisions, are dependent on the complexity of the sensory scene.

KEY WORDS: Cognitive load, Mate choice, Multimodal signalling, Noise, Túngara frog

INTRODUCTION

Communication is a critical component of animal behaviour. It mediates a wide range of tasks and is especially important in mate choice. For species that rely on acoustic signals, background noise is ubiquitous. Sources include biotic noise from vocalising animals, abiotic noise such as rain, and increasingly, anthropogenic disturbance. If background noise levels are high or overlap spectrally with conspecific acoustic signals, they can degrade the receiver's ability to identify and discriminate among individual signallers (Bee and Micheyl, 2008; Vélez and Bee, 2010; Wiley, 2015).

In addition to acoustic signals, many species recruit additional components (e.g. visual components) into their communication system, generating multimodal signals (Candolin, 2003; Higham and Hebets, 2013). The ubiquity of multimodal signals and their importance influencing the response of receivers has been

appreciated for over two decades (Hebets and Papaj, 2005; Partan and Marler, 1999). One common assumption is that multimodal signals evolved as a mechanism to improve the efficacy of communication in noisy environments. For example, if the acoustic channel becomes too noisy, the receiver can increase reliance on a visual signal component (Partan, 2017). Thus, multiple components can provide a level of redundancy or degeneracy (Hebets et al., 2016), improving signal detection and favouring the evolution of complex signals.


Neurobiology and human psychophysics have demonstrated that multimodal signals are integrated by the receiver and this integration is critically important for perception and decision-making (Stein, 2012). In mammals, processing of information from separate sensory channels is strongly integrated in the brain, and this integration is important for helping individuals parse out signal sources in a complex sensory world (Alvarado et al., 2009; Harris and Mrsic-Flogel, 2013; Wallace et al., 2004). For example, human listeners commonly lip read in noisy environments, improving speech comprehension (Sumbly and Pollack, 1954). This multisensory integration has the potential to generate false perceptions, however. Human listeners perceive changes in speech sounds when confronted with the visual component of lips that are mouthing a different sound (e.g. the McGurk effect; McGurk and MacDonald, 1976). Human lips, like other ancillary communication events in nature (e.g. bill movement in singing birds), did not evolve to increase information transfer. Receivers are under selection, however, to glean as much information as possible when making fitness consequential decisions like mate choice. Additional information has the potential, however, to cognitively overwhelm the receiver, and thus more information may not always be better (Alsius et al., 2005; Clark and Dukas, 2003). Despite advances in understanding multisensory integration, little is known about how non-human animals integrate multiple signal components for decision-making, particularly in noisy choice environments.

Anuran amphibians are an excellent system to study how mate choice decisions are made in complex sensory environments. Most species communicate with acoustic signals and commonly do so in noisy environments consisting of both conspecific and heterospecific advertisement signals. Female frogs respond readily with phonotaxis to playbacks of male advertisement calls, generating a clear behaviour that can be used to assess mate preferences. Many frogs also recruit visual and vibratory components into their communication system (Caldwell et al., 2010; Halfwerk et al., 2014; Stamberger et al., 2014). The túngara frog, *Physalaemus pustulosus*, has been the focus of mate choice and communication studies for over 30 years and both female mate preferences and auditory processing have been well studied (Hoke et al., 2007; Ryan, 1985; Ryan et al., 1990; Taylor et al., 2019). This small Neotropical frog is common throughout Middle America and northern South America. During the rainy season (May to November in Panama), male túngara frogs gather nightly at small ephemeral ponds and produce vocalisations to attract mates. The acoustic signal (call) has two components. Each call

¹Department of Biology, Salisbury University, Salisbury, MD 21801, USA.

²Smithsonian Tropical Research Institute, Apartado 0843-03092 Balboa, Ancón, Republic of Panama. ³Department of Integrative Biology, University of Texas, Austin, TX 78712, USA. ⁴Department of Ecological Science, VU University, Amsterdam 1081 HV, The Netherlands.

*Author for correspondence (rctaylor@salisbury.edu)

 R.C.T., 0000-0003-3173-5432; R.J.L., 0000-0002-8139-1589; K.M.M., 0000-0002-6101-1577

consists of a frequency-modulated ‘whine’ and can be appended by one to seven shorter notes called ‘chucks’. The whine is necessary and sufficient to attract mates, but chucks increase attractiveness and are added when vocal competition increases among males (Bernal et al., 2009). Female túngara frogs prioritise the vocal signal, but also attend to the inflating movements of the male vocal sac. All else being equal, females prefer calls accompanied by a visual stimulus of the vocal sac (Taylor et al., 2008).

On any given night, the number of male callers at a pond may range from a single male to dozens calling in close proximity. As additional males join the chorus, vocal competition intensifies, creating a loud din of noise. This creates a ‘cocktail party’-like problem where increased noise levels interfere with the female frogs’ ability to discriminate among callers and choose a mate (Bee, 2012; Bee and Micheyl, 2008). Although several studies have demonstrated the influence of both acoustic properties and visual components on mate choice decisions in the túngara frog (Ryan and Rand, 2003; Taylor et al., 2011; Taylor and Ryan, 2013), we still have a relatively poor understanding of how mate choice decisions are made under noisy conditions.

Despite widespread interest in the evolution of multimodal signals, virtually nothing is known about the role of sensory integration in parsing communication signals embedded in noise. An important hypothesis from multimodal signal theory predicts that additional components will improve signal detection or discrimination in complex sensory environments (Hebets and Papaj, 2005; Rowe, 1999). Under this hypothesis, signal receivers should perform difficult discrimination tasks better when more information is available. In human performance studies, however, additional information has actually been shown to degrade performance in some cases (Endsley, 2000). Here we tested the general hypothesis that female túngara frog responses to preferred male calls are improved when a visual component is added in noisy conditions. We tested this at two levels of decision complexity (two and three choices).

MATERIALS AND METHODS

General experimental procedures

We collected mating pairs of frogs from locations near the Smithsonian Tropical Research Institute (STRI) field station in Gamboa, Republic of Panama. Frogs were gathered by hand from breeding ponds between 19.00 and 23.00 h during the months of June to August in 2013, 2014 and 2018. Amplectant pairs were placed in plastic bags, labelled by location, and placed into a light-safe cooler for transportation back to the laboratory. The frogs were collected in pairs to ensure female motivation during mate choice tests. We kept the frogs in the cooler for at least 1 h before testing to ensure that they were not exposed to light after initial collection. The laboratory was kept in complete darkness when the frogs were being handled to avoid bleaching their photoreceptors. We also

maintained the temperature in the laboratory at 26–28°C to mimic the outside temperature. Light levels in all trials were adjusted to $ca\ 5.5 \times 10^{-10}\ \text{W cm}^{-2}$, similar to moonless light levels commonly experienced by frogs at the breeding pond (Taylor et al., 2008).

Experiments were conducted in a sound attenuation chamber (ETS-Lindgren, Austin, TX, USA), containing speakers and a funnel to restrain females at the start of each trial. The speakers broadcast a pair of natural calls antiphonally with an interval between calls of 1 s. The calls were previously shown to be relatively attractive or unattractive (Fig. 1) (Ryan and Rand, 2003). We played digital sound files using Adobe Audition 2.0 and amplified by NAD Electronics amplifiers. Some experimental treatments included the addition of background noise to the stimulus calls. In these treatments, a wall-mounted speaker (125 cm above the floor) broadcast white noise that was band-filtered to match the frequency spectrum of natural túngara frog calls. Specifically, the spectral band spanned 200–4000 Hz. The dominant frequency of the túngara frog whine ranges from 900 to 400 Hz and the chuck is around 2300 Hz. Both call components have harmonics at additional frequencies, but our white noise band covered virtually the entire frequency range of the male calls. Mounting the noise-generating speaker in the middle of the sound chamber and above floor level ensured that the noise levels were relatively uniform across the test arena. We measured and calibrated all sound pressure levels at the point of the female’s position under the funnel using an Extech sound pressure level (SPL) meter (fast, C-weighting). Some experimental treatments also employed the use of visual components. For this, we placed a highly realistic robotic frog (hereafter robofrog) in front of one or more speakers. A computer-activated piston inflated the robofrog vocal sac synchronously with the call produced at the speaker (for details, see Klein et al., 2012). This provided females with a multisensory display of a calling male, and has been successfully employed in previous studies of multimodal signalling in the túngara frog (Taylor et al., 2008, 2011; Taylor and Ryan, 2013).

To begin each trial, we placed a female under a visually and acoustically transparent funnel in the middle of the chamber. We initiated the sound and/or robofrog playbacks and allowed the female to acclimate under the funnel for 2 min. We then remotely raised the funnel from outside the chamber, and allowed the female to approach a speaker and/or robofrog, indicating her mate choice. We scored a choice when a female approached within 5 cm of a speaker or robofrog (Fig. 2) and remained there for at least 3 s. We documented the choice made by each individual as well as the amount of time it took for her to respond (latency). A trial was discarded from the dataset if the female did not approach a stimulus within 10 min (presumably due to lack of motivation by that female). All behavioural trials were viewed and recorded via an overhead infrared camera mounted to the ceiling of the chamber and connected to Ethovision software.

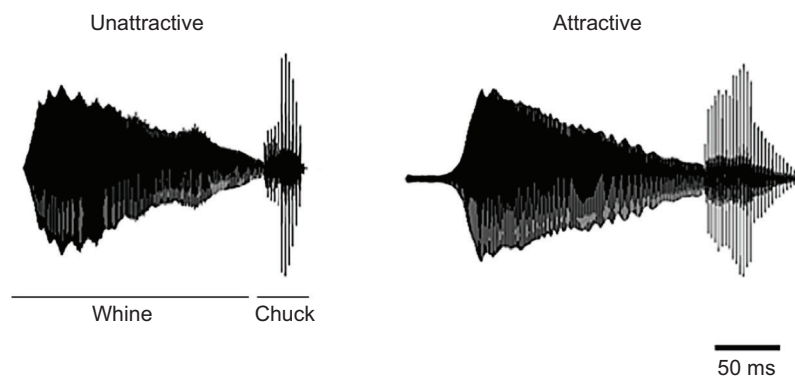


Fig. 1. Exemplar waveforms of one unattractive and one attractive pair of túngara frog calls, one unattractive and one attractive. Females prefer calls (attractive) that are lower in frequency and contain more energy in the chuck.

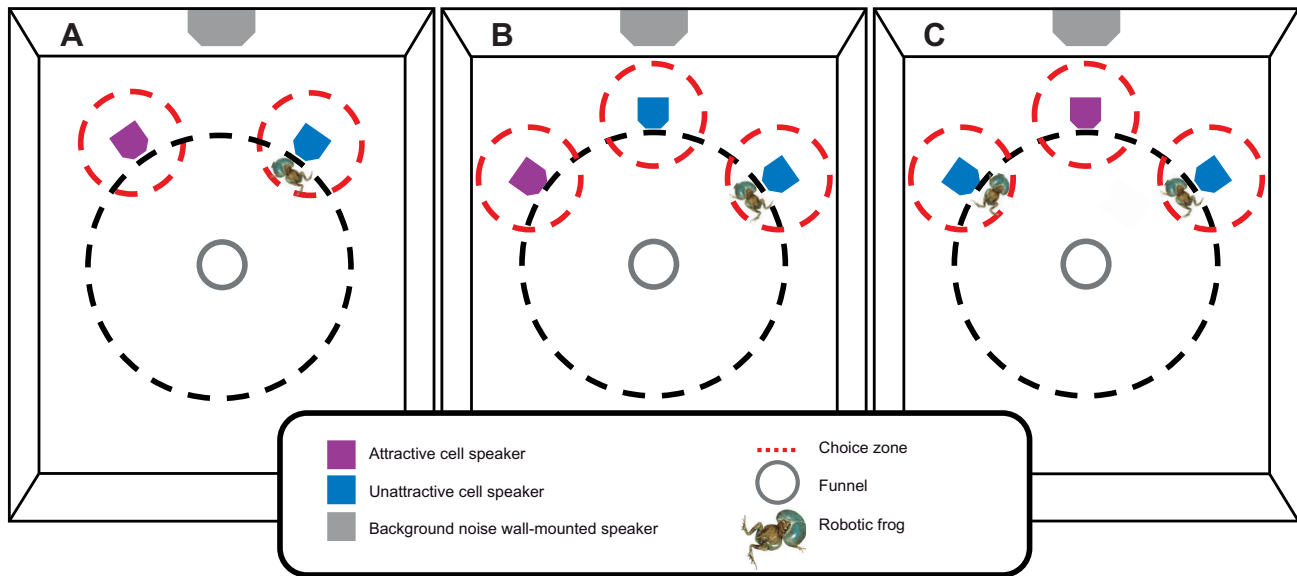


Fig. 2. Set-up of phonotaxis experiments inside the sound chamber. This diagram is not to scale. (A) Measuring female preferences during two-choice tests. Presence and absence of the robofrog, as well as background noise, varies based on treatments. Position of the attractive (purple) and unattractive (blue) call speakers were randomised throughout each treatment, and the robofrog was always located in front of the unattractive speaker. The two speakers were placed equidistant from the central plastic funnel at a distance of 80 cm, and the speakers were separated by a 70 deg angle. (B) Measuring female preferences during three-choice tests. Presence and absence of the robofrog, as well as background noise, varied based on treatments. Background noise is broadcast at high levels for all noise treatments. Location of the attractive call speaker (purple) as well as the location of the robofrog (always in front of an unattractive speaker) was randomised for each trial. (C) The set-up of the double robofrog treatments. In all treatments, the three speakers were placed equidistant from the central plastic funnel at a distance of 80 cm and a 55 deg speaker angle. The choice zone measures 5 cm in all directions around each speaker.

After a night of experiments, we recorded morphological data and identification information for every male and female before returning them to the sites where they were collected. This included mass, snout–vent length (SVL), collection site and recapture dates (if applicable) for each frog. The frogs were toe-clipped according to their four-digit identification number to eliminate the possibility of re-testing individuals on subsequent nights. The toe clips were stored in 1.5 μ l microcentrifuge tubes in 70% ethanol for future DNA extraction and ongoing genetic analyses.

Two-choice tests

In this set of experiments, we presented females with a choice between two speakers (or speaker–robofrog combination) to test the combined effect of noise and visual components on female mate preferences. A total of eight natural call pairs were used to test preferences and each call pair contained one attractive and one unattractive call. These calls are representative of the range of acoustic characteristics (e.g. frequency, duration of the whine, duration of the chuck, etc.) within the species, and their relative attractiveness has been previously determined (Ryan and Rand, 2003). The call stimuli were recordings of natural calls in the field. A total of 16 calls were put together as eight pairs, known to differ in attractiveness (Ryan and Rand, 2003). The same eight pairs were used across all experiments. All calls consisted of a whine followed by a single chuck. This controlled for the strong preference that females express for a whine–chuck over an isolated whine. Each pair was presented to four female frogs. Each female was tested on only one call pair ($N=32$ unique females tested across the eight pairs in each treatment). This design allowed us to test population-level female preferences over the natural range of call variation occurring in nature. The difference in call attractiveness across the pairs resulted primarily from differences in dominant frequency and chuck amplitude. Detailed information about these calls and preference functions can be found in Ryan and Rand (2003).

Two speakers (Mirage Nanosat) were placed equidistant from the funnel at 0.8 m and separated by a 70 deg angle (Fig. 2). Each speaker played either an attractive or unattractive call to the female, and the calls alternated at 1 s intervals on a loop. Although female preferences for the natural call pairs were previously tested, we conducted a control experiment again to verify the strength of female preferences for these same calls ('quiet control'; Fig. 3). This experiment was a simple two-choice test, conducted in the absence of a robofrog or background noise. In subsequent treatments (Fig. 3), we tested female preferences for the same calls in the presence of background noise and added the robofrog visual component. Noise treatments broadcast chorus noise from a centrally located wall-mounted speaker. Multimodal treatments were like the noise treatments, but with a robofrog visual component always placed with the unattractive call.

Stimulus calls broadcast by the speakers were always set at 82 dB SPL (re. 20 μ Pa), measured from the female's release point. The wall-mounted background noise speaker was calibrated to either 79 or 82 dB SPL. This produced a 'low noise' and 'high noise' treatment. In the low noise treatment, the signal was 3 dB higher than the background noise (signal-to-noise ratio: +3 dB); in the high noise treatment, the background noise amplitude was equal to the signal (signal-to-noise ratio: 0 dB). Both noise levels are within the range of natural noise amplitudes of choruses recorded in the field. We tested 32 females per experiment (eight stimulus pairs, four frogs per pair). No female was tested more than once.

Three-choice tests

This experiment largely repeated the two-choice tests, but involved a series of three-choice phonotaxis treatments to test female mate choice preferences under more complex sensory scenes. Female túngara frogs commonly choose from among more than two males, thus we designed this experiment to mimic the more complex conditions that commonly occur in nature (Lea and Ryan, 2015). The same eight call pairs from the two-choice experiment were

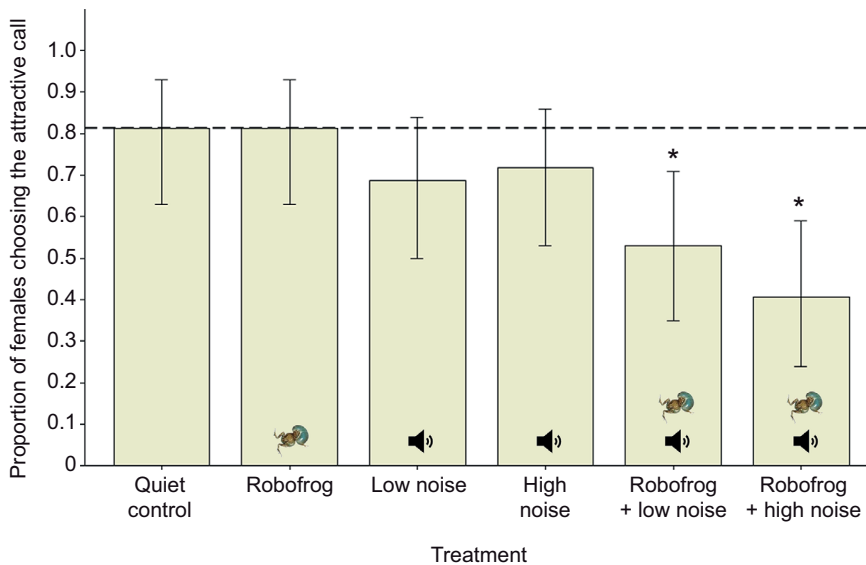


Fig. 3. Responses to the attractive versus unattractive calls in two-choice tests. Values represent the proportion of individuals choosing the attractive call in each treatment. The túngara frog graphic represents treatments with a visual stimulus, and the speaker graphic represents the treatments with added background noise. All call speakers were broadcast at 82 dB while the wall-mounted background noise speaker was broadcast at either 79 dB (low noise) or 82 dB (high noise). The dashed line indicates the expected proportion of choices for the attractive call speaker based on the quiet control treatment. *Significant differences from expected response at $P < 0.05$ from the binomial test. Column bars are Clopper–Pearson 95% confidence intervals.

used. In each three-choice test, one speaker played the attractive call and the other two speakers played the identical unattractive call.

There were six different treatments for this experiment, each with a sample size of 64 (eight stimulus pairs, eight frogs per pair). Doubling the sample size from the two-choice tests was necessary to ensure that each call type–robofrog combination was presented an equal number of times at each speaker position, thereby controlling for position bias. Each treatment had three speakers, placed equidistant from the central plastic funnel at a distance of 0.8 m and separated by a 55 deg angle (Fig. 2). This was the maximum, equal spacing separation we could generate in the sound chamber, but the distance between the speakers was still within the range of natural male spacing in the field. All acoustic stimuli were calibrated to play at 82 dB SPL at the position where the female was released. No female was tested more than once per trial.

An acoustic-only (quiet) control treatment was used to establish baseline preferences for an attractive call versus two identical unattractive calls, in quiet conditions without a visual component. The multimodal treatments involved placing a robofrog in front of one (robofrog) or both (double robofrog) of the unattractive call speakers (Fig. 2). This visual component provided another source of information that females could potentially use when discriminating between calls. Adding the robofrog to the attractive speaker would probably have only increased response to the attractive call in all conditions (Taylor et al., 2008). In nature, not all males are visually assessable to females as variation in vegetation or topography can visually obscure some callers. Thus, our experimental design was relevant to natural conditions. As in the two-choice experiments, noise was broadcast from a wall-mounted speaker at the same sound pressure level as the acoustic calls (82 dB SPL). This is the ‘high’ noise level used previously and was chosen because females performed similarly at both noise levels in the two-choice tests. Patterns of the eight call pairs, placement of attractive and unattractive call speakers, and placement of the visual component were randomised to minimise position bias. In addition, each of the three speakers broadcast an attractive call an equal number of times. In the robofrog treatments, robofrogs were placed with an unattractive call at each speaker position an equal number of times.

Statistical analyses

We tested the hypothesis that the strength of a known preference for an attractive call was influenced by the addition of visual stimuli and

noise. We used a binomial test to determine statistical deviance from expected values. We set the expected response values as the proportion of females that responded to the attractive call in the quiet control treatments: 26:6 (0.8125) in the two-speaker tests and 37:27 (0.578) for the three-speaker tests. Significance levels were reported as mid- P -values, calculated using statistical software from SISA Statistics (<https://www.quantitativeskills.com/sisa/distributions/binomial.htm>). The use of mid- P -values has been advocated as a method for smoothing P -value calculations in categorical data analysis (Agresti, 2001).

We used ANOVA to compare mean latency to choice, to determine whether increased complexity of the sensory environment influenced choice latency. The latency data were not normally distributed, so we conducted a capability analysis of multiple samples. We used the optimised lambda value of a Box–Cox transformation to meet the normality and equal variances assumptions of ANOVA. We also did multiple comparisons among treatments using Tukey’s test.

We also examined speed–accuracy trade-offs for females across treatments. When detection and decision tasks become more difficult, organisms ranging from ants to humans exhibit predictable trade-offs in either decision speed or decision accuracy (Heitz, 2014). In addition to the standard statistical analyses, we also determined if either decision accuracy (proportion choosing the attractive speaker) or latency to choice declined as the sensory complexity of our experiments increased. A performance decline in one of these tasks indicates that the cognitive load on females was increased in a particular treatment.

Ethical note

These experiments were all conducted with permission and in accordance with the animal care and use protocol of the Salisbury University Institutional Animal Care and Use Committee (IACUC), the American Society of Ichthyologists and Herpetologists ‘Guidelines for Use of Live Amphibians and Reptiles in Field and Laboratory Research’ and the Smithsonian Tropical Research Institute IACUC (permit numbers 2011-0825-2014-02, 2014-0101-2017 and 2018-0411-2021). The Ministry of the Environment of Panama (MiAmbiente) provided collecting permits (numbers SE/A-47-13, SE/-45-14 and SEX/A-63-18). Our extensive experience with túngara frogs, including toe-clipping, indicates that handling does not adversely affect survivorship or reproductive behaviour. We

commonly recapture animals actively breeding weeks or months after their initial capture.

RESULTS

Two-choice tests

We first determined baseline female mate preferences for eight pairs of natural calls to determine their relative attractiveness under quiet background conditions. Females expressed a significant preference for a specific set of ‘attractive’ calls under quiet control conditions in the absence of noise and visual components (26:6 in favour of attractive calls; binomial test, $P=0.0004$, compared with an expected 0.5; Fig. 3). The proportion of females responding to the attractive calls in this experiment (81.25%) was identical to previously demonstrated preferences for these same calls (Ryan and Rand, 2003). This demonstrates that the strength of preference for the attractive calls is consistent and repeatable. It supports our use of an expected response 0.8125 to the attractive calls as the null hypothesis to determine if there was a treatment effect from noise or visual components.

For the remaining experiments, we tested female preferences for the same call-pairs in five treatments in which we varied the presence and absence of visual components (robotic frog) as well as background noise levels (band-filtered white noise). When we pitted attractive calls against unattractive calls that were visually enhanced with a robofrog, the visual stimulus failed to alter mate preferences and females retained a robust preference for the attractive calls (26:6, binomial test, $P=0.91$; Fig. 3). Next, we tested female preference for the same call-pairs in the presence of background noise. The presence of noise did not significantly reduce female responses to the attractive calls at either level. In the low-noise treatment, the response to the attractive versus unattractive calls was 22:10 (binomial test, $P=0.089$) and in the high-noise treatment the response was 23:9 (binomial test, $P=0.142$; Fig. 3).

We conducted another experiment with our stimulus pairs, but this time a robofrog was paired with an unattractive call at the low background noise level. Here, the number of females responding to the attractive calls decreased significantly, with nearly equal numbers of frogs responding to the attractive versus unattractive calls (17:15; binomial test, $P=0.0002$; Fig. 3). Finally, we conducted this multisensory experiment with the robofrog again placed at the unattractive speaker, but at the high background noise level.

Females reversed their responses, relative to the quiet control, with significantly more females responding to the relatively unattractive multisensory stimulus (13:19; binomial test, $P<0.0001$; Fig. 3).

Three-choice tests

To increase complexity of the sensory environment, we asked females to choose among three speakers instead of two. We began by again determining the baseline response rate for a single attractive call in the presence of two unattractive calls. In the quiet control, the proportion of responses to the attractive calls was lower than in the two-choice experiments. This was expected as choosing among three options should be inherently more difficult than choosing between two. Females still responded to the attractive calls significantly more often than expected by chance (37:27 in favour of attractive calls; binomial test, random chance=0.33, $P<0.0001$; Fig. 4). This again confirmed female preferences for the attractive calls and provided an expected response proportion in the three-speaker tests (expected=0.578). As with the two-choice experiments, we again wanted to know how visual components, noise, and their combination influence mate responses to an attractive call. Thus, we used the expected null value of 0.578 for the remaining binomial tests.

The remaining treatments in the three-speaker experiment increased the sensory complexity by adding one or more visual components (robofrog) as well as background noise. When a robofrog was added to one of the unattractive call speakers, the visual component did not significantly change responses to the attractive call (40:24 in favour of attractive calls; binomial test, $P=0.489$; Fig. 4). We repeated this multimodal experiment, but added a robofrog at both speakers that were broadcasting the unattractive calls (double robofrog). This also did not significantly change responses to the attractive calls (38:26 in favour of attractive calls; binomial test, $P=0.85$; Fig. 4). We then added background noise (i.e. high noise level) for the next three treatments. In the presence of background noise, but without visual stimuli, females chose the attractive call significantly less often than expected (27:37, binomial test, $P=0.013$; Fig. 4). When we added a visual component (robofrog) to the noisy choice environment, the females also exhibited a significantly reduced response to the attractive calls (26:38; binomial test, $P=0.006$; Fig. 4). Finally, we added the second robofrog (double robofrog) so both unattractive speakers presented equal multisensory displays in the presence of background noise. Here, the females did

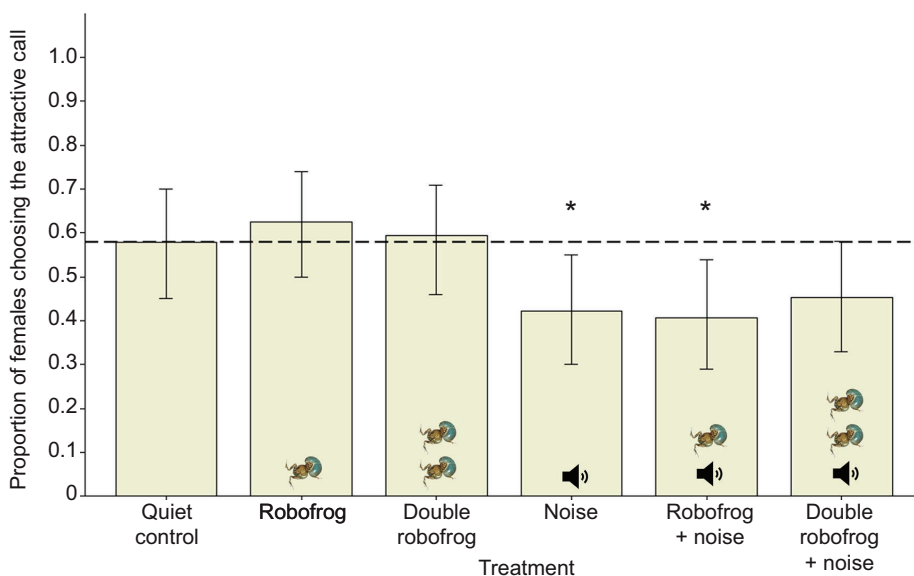


Fig. 4. Responses to the attractive versus unattractive calls in three-choice tests. The túngara frog graphic represents treatments with a visual stimulus and the speaker graphic represents the treatments with added background noise. All acoustic stimuli were broadcast at 82 dB. Noise was broadcast at 82 dB yielding the same acoustic conditions as the high-noise treatment in the two-choice tests. The dashed line indicates the expected proportion of choices for the attractive call speaker based on the quiet control treatment. *Significant differences from expected response at $P<0.05$ from the binomial test. Column bars are Clopper–Pearson 95% confidence intervals.

not show a significantly reduced response to attractive calls, but numerically, still did not choose the attractive call as often as expected (29:35; binomial test, $P=0.05$; Fig. 4). In other words, there was still a reduction (non-significant trend) in the proportion of females choosing the attractive call.

Latencies

In addition to finding different responses to attractive calls, we also compared choice latencies across treatments. We used an optimised lambda value of 0 for the two-choice test experiment and lambda of -0.2 for the three-choice test experiment to transform the data to fit assumptions of normality and equal variances. We found no significant latency difference between any of the treatments in the two-choice tests (quiet control: 114.1 ± 15.0 s, mean \pm s.e.m.; robofrog: 141.6 ± 18.0 s; low noise: 128.8 ± 24.6 s; high noise: 112.8 ± 17.5 s; robofrog+low noise: 106.4 ± 19.3 s; robofrog+high noise: 81.2 ± 13.9 s; ANOVA, $P=0.351$). Thus, none of the noise or noise–visual combinations significantly changed response times.

We did find a significant latency difference between treatments for the three-choice tests (Fig. 5; quiet control: 99.7 ± 10.5 s; robofrog: 80.5 ± 8.84 s; double robofrog: 91.9 ± 8.06 s; noise: 124.4 ± 16.0 s; robofrog+noise: 104.7 ± 13.4 s; double robofrog+noise: 76.9 ± 12.7 s; ANOVA, $P=0.001$). When comparing the mean latencies for all three-choice treatments, we found that the double robofrog+noise treatment resulted in significantly shorter latencies than the quiet control, noise and robofrog+noise treatments (Tukey's pairwise comparisons, $P=0.015$). A similar (non-significant) trend was seen in the two-choice tests.

DISCUSSION

An enormous body of work has demonstrated the importance of female mate choice in the evolution of male sexual signals (Rosenthal, 2017). Despite this progress, we still have a poor understanding of how choice operates in complex sensory scenes and many experiments probably over-estimate the strength of preference functions (Tanner and Bee, 2020). In this study we conducted a series of experiments to address the role of sensory complexity on mate choice decisions. Previous work on multimodal displays in túngara frogs demonstrated that between two equally attractive calls, females prefer the call that is enhanced with a visual component of a calling male (Taylor et al., 2008; Stange et al., 2017). Ryan and Rand (2003) showed that females express a strong preference for specific natural

calls and we confirmed that preference again in this study. This preference was maintained for 17 years. Given this robust, repeatable preference for 'attractive' calls (see also Ryan et al., 2019), and a visual component of a calling male, we first wanted to test the hypothesis that the visual component increases the attractiveness of an otherwise unattractive call. In the absence of noise, it did not. This was true in both two- and three-choice tests. The vocal sac has also been shown to strongly modulate female preference for calls, depending on light conditions (Cronin et al., 2019) and the degree of temporal synchrony between the vocal sac movement and call (Taylor et al., 2011; Taylor and Ryan, 2013). Collectively, these data show that the vocal sac plays an important role in modulating female mating decisions (Reichert and Höbel, 2015), but it does not act as a simple ornament, in the classical sense of sexual selection (Burley and Symanski, 1998), by adding attractiveness to an otherwise unattractive call.

A common prediction is that multimodal signals have been favoured by selection because they increase communication efficacy in noise; our data here do not support this hypothesis. In two-choice tests, females failed to retain a preference for the attractive calls in the presence of noise and a robofrog. If the visual component merely improves auditory discrimination in noise (as seen in some human psychophysical studies, e.g. Lovelace et al., 2003), then females should have retained a preference for the attractive call, even with the robofrog placed at the unattractive call. This was not the case. When our robofrog was coupled to the unattractive call in noise, females shifted their preference towards the unattractive calls. One explanation for the shift to the unattractive call in noise is that females may rely more heavily on the visual component when the auditory channel becomes noisier. Partan (2017) referred to this as 'switching channels'. In order for channel switching to occur, two things are required. First, each signal component must be redundant; second, signal transmission in one channel must be impaired (Partan, 2017). The male túngara frog's vocal sac does not provide redundant information to the call (Taylor et al., 2008). In addition, our data here demonstrate that the noise treatments did not substantially impair the females' auditory channel. If noise in the auditory channel impairs a female's ability to discriminate among calls, this would be revealed in the speed–accuracy trade-off. That is, acoustic masking should result in declines in either decision accuracy or increases in decision time (Chittka et al., 2009). With two choices in the presence of background noise, and absent visual components, females showed no significant

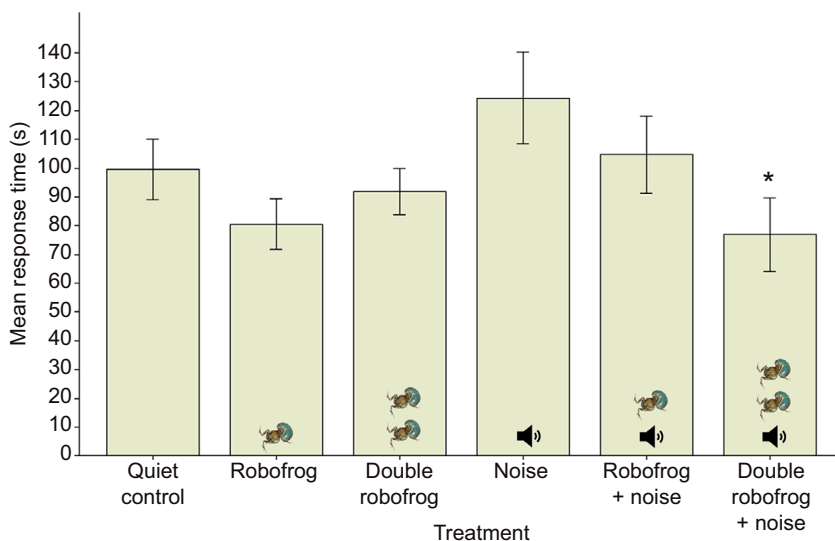


Fig. 5. Latency to choice compared with the control in the three-choice tests. The túngara frog graphic represents treatments with a visual stimulus. The speaker graphic represents the treatments with added background noise. The error bars around the mean latencies indicate the s.e.m. for each treatment. *Significance at $P<0.05$, representing only the treatments that have shorter latencies than the control, based on Tukey's pairwise comparisons.

decrease in decision accuracy. They also showed no significant increase in decision time, thus auditory processing was not substantially impaired (see Hemingway et al., 2019). Even though noise levels were of relatively high amplitude, the position of the noise speaker mounted on the wall probably generated spatial release from masking (Bee, 2008). That is, the separation of noise sources between speakers probably allowed females to detect the signals, despite having to contend with auditory processing of the noise. In two-choice tests, the shift in preference towards the visual component in the presence of noise was therefore not due to females switching reliance on components, as occurs in many species (Gomes et al., 2016; Partan, 2017). One possible explanation is that in the presence of noise, the robofrog merely acted as a distractor, reducing response to the attractive call. Females were able to maintain both speed and accuracy in the independent noise and visual treatments, however. The added cognitive task generated by the two components together did reduce decision accuracy, possibly cognitively overloading the females. Alternatively, the presence of noise may have generated a shift in how females perceived the call. This is similar to the audio-visual shift that occurs in the human McGurk effect (McGurk and MacDonald, 1976) and the stream-bounce illusion, when the perception of objects passing through each other changes to 'bouncing off' when a sound is added (Sekuler et al., 1997).

Based on data from experiments in the absence of background noise, Taylor and Ryan (2013) suggested that the vocal sac was co-opted into the acoustic communication display by the receiver as a means to increase discrimination among callers in noise, analogous to human lip readers at a cocktail party. The two-choice data do not support this visual redundancy in noisy environments. It is likely that the female response to the vocal sac was co-opted from a pre-existing bias for movement in the anuran visual system (e.g. anuran visual systems are acutely sensitive to motion; Lettvin et al., 1959). Data show that the vocal sac does improve acoustic signal recognition (Taylor and Ryan, 2013), but this appears to be limited to relatively simple acoustic mating scenes. In more complex acoustic environments (e.g. continuous noise that is common in frog choruses), the cognitive load on multisensory processing may alter perceptions or even lead to a breakdown (Lavie, 2005; Tsetsos et al., 2010) such that the vocal sac no longer improves signal discrimination. This reduction in decision-making accuracy was surprising.

Next, we scaled up the complexity of the experimental mating scene by presenting females with a series of three-choice tests. We essentially repeated our two-choice experiments (at the high noise level), but gave females a choice between three calls. In a three-choice test without any noise or visual components, females maintained a significant preference for the attractive call. Unlike the two-choice experiments, however, the accuracy of female choice significantly declined in the presence of noise alone. When presented with three choices in noise, only 42% of females chose the attractive call and this was significantly worse than expected. This suggests that, in the presence of noise, the increased choice complexity generated a cognitive task load that prevented females from expressing their preference for attractive calls. In quiet conditions, when females were presented with a robofrog at either one or both of the unattractive speakers, females maintained a preference for the attractive calls (62.5% single and 59.4% double).

We predicted that the addition of a robofrog visual component would rescue the female preference for attractive calls in a three-choice test with noise. From a (multimodal) signal detection standpoint, the additional visual component should make detecting the attractive call easier in noise. When females were presented with one attractive and two unattractive calls and a robofrog at one speaker, female responses

to the attractive call remained significantly lower than expected when no noise was present. We added a second treatment with two robofrogs, one at each unattractive call with background noise. We predicted that this should be an easier discrimination test than the single robofrog because the unattractive speakers were standardised with respect to the visual stimulus. In this case, female responses were not significantly different from expected. Statistically, the effect of the double robofrog helped maintain preference for the attractive calls in noise ($P=0.05$). The actual effect of improving call discrimination in favour of the attractive call was small, however, and female performance was similar to all treatments containing noise.

In sum, noise itself did not significantly decrease female responses to attractive calls in two-choice tests, but did so in a three-choice test. In two-choice tests, females reduced their responses to the attractive calls only in the simultaneous presence of noise and the visual component. In three-choice tests the addition of noise reduced female responses to the attractive call and this diminished response largely remained even when visual components were added to an unattractive call. Unlike our two-choice tests, the primary influence on the degradation of female responses in three-choice tests was noise. In no test did the visual component strongly enhance female responses to the attractive call in noise. Females did exhibit the fastest choices in the double robofrog+noise treatment (Fig. 5). This suggests that the standardisation of the two unattractive calls reduced the cognitive load in the three-choice test and improved the females' discrimination ability. Again, however, the improvement in discrimination was marginal in this treatment.

Despite contrary evidence in some systems (Kulahci et al., 2008), our data show that multimodal displays do not always improve receiver performance in noise (Rubi and Stephens, 2016). In two-choice tests, declines in responses to the attractive calls did not follow increasing task difficulty, e.g. picking the attractive calls should be more difficult in noise (Fig. 3), but did in three-choice tests (Fig. 4). This suggests that different perceptual processes may be occurring, dependent on the complexity of the sensory scene. In simpler two-choice tests, we rule out 'channel switching' due to the lack of speed accuracy trade-offs, and the frogs behaved as if they were experiencing a perceptual 'McGurk-like' effect or a cognitive overload. In more complex three-choice tests, the shift away from responding to the attractive calls was driven primarily by the noise itself. Interestingly, data from the two-choice tests are consistent with neurophysiological changes known to occur in the anuran auditory system in noise. In the spring peeper, for example, females exhibit neural modulations in the auditory midbrain and also show changes in mating preferences when exposed to background noise (Schwartz and Gerhardt, 1998). In the green treefrog, exposure to chorus noise increases auditory midbrain receptivity, thus modulating auditory responses to conspecific mating signals (Gall and Wilczynski, 2014).

Our results are also similar to emergent perceptions that appear when human listeners are presented with entangled audio-visual signals (Bahrick et al., 2004; Lavie, 2005). Also, a recent study demonstrated that barn owls conduct visual grouping tasks similar to humans, even though they possess a different neural architecture (Zahar et al., 2018). This suggests that birds and mammals may share cognitive mechanisms for perceptual grouping (Farris and Taylor, 2016), arising from common ecological needs of finding food and mates. Our data here suggest this may be true of amphibians as well. If multimodal signals do not improve mate choice decisions in noise, then why did they evolve? Quite simply, the visual component may have been recruited from a 'hidden landscape' of preference arising from sensory biases of the anuran visual system (Reichert et al., 2017; Rowe and Guilford, 1996).

Even though we lack a full understanding of the neurophysiological processes at work, we demonstrate that acoustic noise dynamically influences the expression of female mating preferences in a multimodal communication system. The level of chorus noise varies tremendously in natural túngara frog choruses; depending on the number of males that attend the chorus, background noise ranges from almost none to a continuous drone. Females are regularly confronted with a range of signal discrimination tasks, thus mate choice outcomes are likely to fluctuate dynamically with background noise and this includes variation in visual components. Also, because the presence of background noise can change female mate preferences, increasing urbanisation may influence multisensory communication systems in previously unappreciated ways (Halfwerk et al., 2019) and this topic itself deserves additional investigation.

Acknowledgements

We thank A. Dunn for help with data collection and experimental set-up. Two anonymous reviewers provided helpful comments that improved the quality of this manuscript. The Smithsonian Tropical Research Institute (STRI) provided logistical support and we are especially grateful for support provided by O. Arosemena, L. Camacho, R. Urriola, A. Villegas, V. Fernandez, T. Parris and V. Bernal.

Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: R.C.T., R.A.P., M.J.R., K.L.H.; Methodology: R.C.T., K.O.W., R.J.L., K.M.M., R.A.P., M.J.R., K.L.H.; Formal analysis: W.H., M.J.R., K.L.H., R.C.T., K.O.W., R.J.L.; Investigation: R.C.T., K.O.W., R.J.L., K.M.M., K.L.H.; Resources: M.J.R., K.L.H., R.C.T., R.A.P.; Data curation: K.O.W., R.J.L., K.M.M., K.L.H., R.C.T.; Writing - original draft: R.C.T.; Writing - review & editing: R.C.T., K.O.W., R.J.L., K.M.M., W.H., R.A.P., M.J.R., K.L.H.; Supervision: R.C.T., R.A.P., M.J.R., K.L.H.; Project administration: R.C.T., R.A.P., M.J.R., K.L.H.; Funding acquisition: R.C.T., R.A.P., M.J.R., K.L.H.

Funding

This work was funded by a National Science Foundation grant (IOS 1120031) to R.C.T., M.J.R. and R.A.P.; a Salisbury University Building Research Excellence grant to R.C.T. and K.L.H.; a Smithsonian Institution Walcott Scholarly Studies grant (34493602) to R.A.P.; and a Salisbury University Graduate Research and Presentation grant to K.O.W. and R.J.L.

Data availability

Raw data can be accessed in the Dryad Digital Repository (Taylor, 2020): vdnjcsxk.

References

- Agresti, A.** (2001). Exact inference for categorical data: recent advances and continuing controversies. *Stat. Med.* **20**, 2709-2722. doi:10.1002/sim.738
- Alsius, A., Navarra, J., Campbell, R. and Soto-Faraco, S.** (2005). Audiovisual integration of speech falters under high attention demands. *Curr. Biol.* **15**, 839-843. doi:10.1016/j.cub.2005.03.046
- Alvarado, J. C., Stanford, T. R., Rowland, B. A., Vaughan, J. W. and Stein, B. E.** (2009). Multisensory integration in the superior colliculus requires synergy among corticocollicular inputs. *J. Neurosci.* **29**, 6580-6592. doi:10.1523/JNEUROSCI.0525-09.2009
- Bahrack, L. E., Lickliter, R. and Flom, R.** (2004). Intersensory redundancy guides the development of selective attention, perception, and cognition in infancy. *Curr. Dir. Psychol. Sci.* **13**, 99-102. doi:10.1111/j.0963-7214.2004.00283.x
- Bee, M. A.** (2008). Finding a mate at a cocktail party: spatial release from masking improves acoustic mate recognition in grey treefrogs. *Anim. Behav.* **75**, 1781-1791. doi:10.1016/j.anbehav.2007.10.032
- Bee, M. A.** (2012). Sound source perception in anuran amphibians. *Curr. Opin. Neurobiol.* **22**, 301-310. doi:10.1016/j.conb.2011.12.014
- Bee, M. A. and Micheyl, C.** (2008). The cocktail party problem: What is it? How can it be solved? And why should animal behaviorists study it? *J. Comp. Psychol.* **122**, 235-251. doi:10.1037/0735-7036.122.3.235
- Bernal, X. E., Akre, K. L., Baugh, A. T., Rand, A. S. and Ryan, M. J.** (2009). Female and male behavioral response to advertisement calls of graded complexity in túngara frogs, *Physalaemus pustulosus*. *Behav. Ecol. Sociobiol.* **63**, 1127-1269. doi:10.1007/s00265-009-0795-5
- Burley, N. T. and Symanski, R.** (1998). A taste for the beautiful: latent aesthetic mate preferences for white crests in two species of Australian grassfinches. *Am. Nat.* **152**, 792-802. doi:10.1086/286209
- Caldwell, M. S., Johnston, G. R., McDaniel, J. G. and Warkentin, K. M.** (2010). Vibrational signaling in the agonistic interactions of red-eyed treefrogs. *Curr. Biol.* **20**, 1012-1017. doi:10.1016/j.cub.2010.03.069
- Candolin, U.** (2003). The use of multiple cues in mate choice. *Biol. Rev. Camb. Philos. Soc.* **78**, 575-595. doi:10.1017/S1464793103006158
- Chittka, L., Skorupski, P. and Raine, N. E.** (2009). Speed-accuracy tradeoffs in animal decision making. *Trends Ecol. Evol.* **24**, 400-407. doi:10.1016/j.tree.2009.02.010
- Clark, C. W. and Dukas, R.** (2003). The behavioral ecology of a cognitive constraint: limited attention. *Behav. Ecol.* **14**, 151-156. doi:10.1093/beheco/14.2.151
- Cronin, A. D., Ryan, M. J., Page, R. A., Hunter, K. L. and Taylor, R. C.** (2019). Environmental heterogeneity alters mate choice behavior for multimodal signals. *Behav. Ecol. Sociobiol.* **73**, 43. doi:10.1007/s00265-019-2654-3
- Endsley, M. R.** (2000). Theoretical underpinnings of situation awareness: a critical review. In *Situation Awareness Analysis and Measurement* (ed. M. R. Endsley and D. J. Garland), pp. 3-21. Mahwah, NJ: Lawrence Erlbaum Associates.
- Farris, H. E. and Taylor, R. C.** (2016). Mate searching animals as model systems for understanding perceptual grouping. In *Psychological Mechanisms in Animal Communication* (ed. M. A. Bee and C. Miller), pp. 89-118, Springer.
- Gall, M. D. and Wilczynski, W.** (2014). Prior experience with conspecific signals enhances auditory midbrain responsiveness to conspecific vocalizations. *J. Exp. Biol.* **217**, 1977-1982. doi:10.1242/jeb.096883
- Gomes, D. G. E., Page, R. A., Geipel, I., Taylor, R. C., Ryan, M. J. and Halfwerk, W.** (2016). Bats perceptually weight prey cues across sensory systems when hunting in noise. *Science* **353**, 1277-1280. doi:10.1126/science.aaf7934
- Halfwerk, W., Blaas, M., Kramer, L., Hijner, N., Trillo, P. A., Bernal, X. E., Page, R. A., Goutte, S., Ryan, M. J. and Eilers, J.** (2019). Adaptive changes in sexual signalling in response to urbanization. *Nat. Ecol. Evol.* **3**, 374-380. doi:10.1038/s41559-018-0751-8
- Halfwerk, W., Dixon, M. M., Ottens, K. J., Taylor, R. C., Ryan, M. J., Page, R. A. and Jones, P. L.** (2014). Risks of multimodal signaling: bat predators attend to dynamic motion in frog sexual displays. *J. Exp. Biol.* **217**, 3038-3044. doi:10.1242/jeb.107482
- Harris, K. D. and Mrsic-Flogel, T. D.** (2013). Cortical connectivity and sensory coding. *Nature* **503**, 51-58. doi:10.1038/nature12654
- Hebets, E. A. and Papaj, D. R.** (2005). Complex signal function: developing a framework of testable hypotheses. *Behav. Ecol. Sociobiol.* **57**, 197-214. doi:10.1007/s00265-004-0865-7
- Hebets, E. A., Barron, A. B., Balakrishnan, C. N., Hauber, M. E., Mason, P. H. and Hoke, K. L.** (2016). A systems approach to animal communication. *Proc. R. Soc. B* **283**, 20152889. doi:10.1098/rspb.2015.2889
- Heitz, R. P.** (2014). The speed-accuracy tradeoff: history, physiology, methodology, and behavior. *Front. Neurosci.* **8**, 150. doi:10.3389/fnins.2014.00150
- Hemingway, C. T., Lea, A. M., Page, R. A. and Ryan, M. J.** (2019). Effects of information load on response times in frogs and bats: mate choice vs. prey choice. *Behav. Ecol. Sociobiol.* **73**, 111. doi:10.1007/s00265-019-2726-4
- Higham, J. P. and Hebets, E. A.** (2013). An introduction to multimodal communication. *Behav. Ecol. Sociobiol.* **67**, 1381-1388. doi:10.1007/s00265-013-1590-x
- Hoke, K. L., Ryan, M. J. and Wilczynski, W.** (2007). Integration of sensory and motor processing underlying social behaviour in túngara frogs. *Proc. R. Soc. B* **274**, 641-649. doi:10.1098/rspb.2006.0038
- Klein, B. A., Stein, J. and Taylor, R. C.** (2012). Robots in the service of animal behavior. *Commun. Integr. Biol.* **5**, 466-472. doi:10.4161/cib.21304
- Kulahci, I. G., Dornhaus, A. and Papaj, D. R.** (2008). Multimodal signals enhance decision making in foraging bumble-bees. *Proc. R. Soc. B* **275**, 797-802. doi:10.1098/rspb.2007.1176
- Lavie, N.** (2005). Distracted and confused?: selective attention under load. *Trends Cogn. Sci.* **9**, 75-82. doi:10.1016/j.tics.2004.12.004
- Lea, A. M. and Ryan, M. J.** (2015). Irrationality in mate choice revealed by túngara frogs. *Science* **349**, 964-966. doi:10.1126/science.aab2012
- Lettvin, J. Y., Maturana, H. R., McCulloch, W. S. and Pitts, W. H.** (1959). What the frog's eye tells the frog's brain. *Proc. IRE* **47**, 1940-1951. doi:10.1109/JRPROC.1959.287207
- Lovelace, C. T., Stein, B. E. and Wallace, M. T.** (2003). An irrelevant light enhances auditory detection in humans: a psychophysical analysis of multisensory integration in stimulus detection. *Cogn. Brain Res.* **17**, 447-453. doi:10.1016/S0926-6410(03)00160-5
- McGurk, H. and MacDonald, J.** (1976). Hearing lips and seeing voices. *Nature* **264**, 746-748. doi:10.1038/264746a0
- Partan, S. R.** (2017). Multimodal shifts in noise: switching channels to communicate through rapid environmental change. *Anim. Behav.* **124**, 325-337. doi:10.1016/j.anbehav.2016.08.003
- Partan, S. R. and Marler, P.** (1999). Communication goes multimodal. *Science* **283**, 1272-1273. doi:10.1126/science.283.5406.1272
- Reichert, M. S. and Höbel, G.** (2015). Modality interactions alter the shape of acoustic mate preference functions in gray treefrogs. *Evolution* **69**, 2384-2398. doi:10.1111/evo.12750

- Reichert, M. S., Finck, J. and Ronacher, B.** (2017). Exploring the hidden landscape of female preferences for complex signals. *Evolution* **71**, 1009-1024. doi:10.1111/evo.13202
- Rosenthal, G. G.** (2017). *Mate Choice: The Evolution of Sexual Decision Making from Microbes to Humans*. Princeton University Press.
- Rowe, C.** (1999). Receiver psychology and the evolution of multicomponent signals. *Anim. Behav.* **58**, 921-931. doi:10.1006/anbe.1999.1242
- Rowe, C. and Guilford, T.** (1996). Hidden colour aversions in domestic chicks triggered by pyrazine odours of insect warning displays. *Nature* **383**, 520-522. doi:10.1038/383520a0
- Rubi, T. L. and Stephens, D. W.** (2016). Does multimodality *per se* improve receiver performance? An explicit comparison of multimodal versus unimodal complex signals in a learned signal following task. *Behav. Ecol. Sociobiol.* **70**, 409-416. doi:10.1007/s00265-016-2061-y
- Ryan, M. J.** (1985). *The Túngara Frog: A Study in Sexual Selection and Communication*. University of Chicago Press.
- Ryan, M. J., Akre, K. L., Baugh, A. T., Bernal, X. E., Lea, A. M., Leslie, C., Still, M. B., Wylie, D. C. and Rand, A. S.** (2019). Nineteen years of consistently positive and strong female mate preferences despite individual variation. *Am. Nat.* **194**, 125-134. doi:10.1086/704103
- Ryan, M. J. and Rand, A. S.** (2003). Sexual selection in female perceptual space: how female túngara frogs perceive and respond to complex population variation in acoustic mating signals. *Evolution* **57**, 2608-2618. doi:10.1111/j.0014-3820.2003.tb01503.x
- Ryan, M. J., Fox, J. H., Wilczynski, W. and Rand, A. S.** (1990). Sexual selection for sensory exploitation in the frog *Physalaemus pustulosus*. *Nature* **343**, 66-67. doi:10.1038/343066a0
- Schwartz, J. J. and Gerhardt, H. C.** (1998). The neuroethology of frequency preferences in the spring peeper. *Anim. Behav.* **56**, 55-69. doi:10.1006/anbe.1998.0737
- Sekuler, R., Sekuler, A. B. and Lau, R.** (1997). Sound alters visual motion perception. *Nature* **385**, 308. doi:10.1038/385308a0
- Stange, N., Page, R. A., Ryan, M. J. and Taylor, R. C.** (2017). Interactions between complex multisensory signal components result in unexpected mate choice responses. *Anim. Behav.* **134**, 239-247. doi:10.1016/j.anbehav.2016.07.005
- Starnberger, I., Preininger, D. and Hödl, W.** (2014). The anuran vocal sac: a tool for multimodal signalling. *Anim. Behav.* **97**, 281-288. doi:10.1016/j.anbehav.2014.07.027
- Stein, B. E.** (2012). *The New Handbook of Multisensory Processes*. Cambridge, MA: MIT Press.
- Sumbly, W. H. and Pollack, I.** (1954). Visual contribution to speech intelligibility in noise. *J. Acoust. Soc. Am.* **26**, 212-215. doi:10.1121/1.1907309
- Tanner, J. C. and Bee, M. A.** (2020). Inconsistent sexual signaling degrades optimal mating decisions in animals. *Sci. Adv.* **6**, eaax3957. doi:10.1126/sciadv.aax3957
- Taylor, R.** (2020). Data from Complex sensory environments alter mate choice outcomes. *Dryad Dataset* doi:10.5061/dryad.vdncjxsk
- Taylor, R. C., Akre, K., Wilczynski, W. and Ryan, M. J.** (2019). Behavioral and neural auditory thresholds in a frog. *Curr. Zool.* **65**, 333-341. doi:10.1093/cz/zoy089
- Taylor, R. C. and Ryan, M. J.** (2013). Interactions of multisensory components perceptually rescue túngara frog mating signals. *Science* **341**, 273-274. doi:10.1126/science.1237113
- Taylor, R. C., Klein, B. A., Stein, J. and Ryan, M. J.** (2008). Faux frogs: multimodal signalling and the value of robotics in animal behaviour. *Anim. Behav.* **76**, 1089-1097. doi:10.1016/j.anbehav.2008.01.031
- Taylor, R. C., Klein, B. A., Stein, J. and Ryan, M. J.** (2011). Multimodal signal variation in space and time: how important is matching a signal with its signaler? *J. Exp. Biol.* **214**, 815-820. doi:10.1242/jeb.043638
- Tsetsos, K., Usher, M. and Chater, N.** (2010). Preference reversal in multiattribute choice. *Psychol. Rev.* **117**, 1275-1291. doi:10.1037/a0020580
- Vélez, A. and Bee, M. A.** (2010). Signal recognition by frogs in the presence of temporally fluctuating chorus-shaped noise. *Behav. Ecol. Sociobiol.* **64**, 1695-1709. doi:10.1007/s00265-010-0983-3
- Wallace, M. T., Ramachandran, R. and Stein, B. E.** (2004). A revised view of sensory cortical parcellation. *Proc. Natl. Acad. Sci. USA* **101**, 2167-2172. doi:10.1073/pnas.0305697101
- Wiley, R. H.** (2015). *Noise Matters*. Cambridge, MA: Harvard University Press.
- Zahar, Y., Lev-Ari, T., Wagner, H. and Gutfreund, Y.** (2018). Behavioral evidence and neural correlates of perceptual grouping by motion in the barn owl. *J. Neurosci.* **38**, 6653-6664. doi:10.1523/JNEUROSCI.0174-18.2018