Body condition and background noise alter female responses to uni- and multimodal signals emitted by a male mimicking robot frog

Vinícius Matheus Caldart[1,2], Maurício Beux dos Santos[3], Glauco Machado[1]

[1] LAGE do Departamento de Ecologia, Instituto de Biociências, Universidade de São Paulo, Brazil

[2] Departamento de Biologia Geral, Universidade Estadual de Ponta Grossa, Brazil

[3] Departamento de Bioquímica e Biologia Molecular, Programa de Pós-graduação em Bioquímica Toxicológica, Universidade Federal de Santa Maria, Brazil

Correspondence

Vinícius Matheus Caldart

Email: viniciuscaldart@gmail.com

Running head: Female body condition, background noise and multimodal communication

FUNDING INFORMATION

VMC was supported by Fundação de Amparo à Pesquisa do Estado de São Paulo (2015/14336-6). GM is supported by Conselho Nacional de Desenvolvimento Científico e Tecnológico (306550/2014-8) and Fundação de Amparo à Pesquisa do Estado de São Paulo (2021/00915-5).

1. Mate choice in females is influenced by intrinsic and extrinsic factors, including signal conspicuity, receiver body condition, and environmental properties. These factors interact in complex ways to modulate the choice of mates. Multimodal signals are more conspicuous than their unimodal components and therefore should elicit a stronger response. However, variations in female body condition and background noise can modify their responsiveness to signals of varying conspicuity.

2. Males of the diurnal stream-dwelling frog *Crossodactylus schmidti* emit unimodal e multimodal signals under variable noisy conditions, and the females vary greatly in body condition. We tested hypotheses on how signal type (unimodal or multimodal) interacts with female body condition and background noise to modify female responses. In a field experiment using a male mimicking robot frog, females were randomly exposed to acoustic-only (call, A), visual-only (toe flag, V), and multimodal (call + toe flag, M) stimuli, while female body condition was estimated and data on background noise was taken.

3. Females exhibited three types of response: emission of acoustic signals, emission of visual signals, and movements toward the robot. All stimuli elicited responses, with a higher percentage of females responding to M, an intermediate percentage to A, and a lower percentage to V. Females in better physical condition exhibited a decreased probability of acoustic response, emitted signals at a lower rate, and took more time to emit signals or move towards the robot. With increasing noise, females exhibited decreased probability of responding with a visual signal to both the visual and multimodal stimuli, but when stimulated by the acoustic stimulus, females exhibited a higher probability of visual response as the noise increased. Finally, females at noisier sites also emitted signals at a higher rate but took more time to respond with visual signals and to move towards the robot.

4. The results suggest that the multimodal signal had the highest female responsiveness. The negative effect of body condition and the positive effect of background noise on the response occurred because better-conditioned females were more selective in their choice, while noisy environments negatively interfered with mate assessment. Our study highlights the complex and context-dependent nature of female mate choice, influenced by signal conspicuity, female body condition, and noise levels.

KEY WORDS: background noise, electromechanical model, female choosiness, female quality, multimodal signaling, sexual selection.

INTRODUCTION

Mate choice is a pervasive pattern in sexually reproducing species and can be described as a nonrandom allocation of reproductive resources from one sex to individuals of the opposite sex (Edward, 2014). Although there is growing evidence that males also engage in mate choice (Bonduriansky, 2001; Edward and Chapman, 2011), this behavior is more intensively studied and understood in females (Andersson 1994; Rosenthal, 2017). Regardless of the sex, mate choice is the manifestation of the mating preference, which is an innate tendency of individuals of one sex to accept mating with individuals of the other sex bearing certain phenotypes (Jennions and Petrie, 1997). However, mate choice is also influenced by intrinsic (condition-dependent) and extrinsic (context-dependent) factors, which affect which individuals are chosen as mates (Cotton et al., 2006; Dougherty, 2023).

Intrinsic factors capable of modulating mate choice include, for instance, age, attractiveness, parasite load, and body condition (examples in Dougherty, 2023). The influence of body condition (sensu Rowe and Houle, 1996) on mate choice can be explained in terms of costs. Females in good body condition can afford to be choosy and spend significant time and energy searching and evaluating potential mates (hereafter mate sampling). Conversely, females in poor body condition are less likely to pay the costs of mate sampling and are expected to mate sooner than females in good condition (Cotton et al., 2006). In fact, lower choosiness (also known as preference strength) in females in poor condition has been reported in some studies. For example, an experimental study with black-field cricket, *Teleogryllus commodus*, showed that females in poor condition have lower choosiness for high-quality male calls than females in good condition (Hunt et al., 2005). Similarly, females of the canary *Serinus* *canaria* that have their body condition experimentally reduced show lower choosiness for high-quality male songs than females in good condition (Lerch et al., 2013).

Extrinsic factors affecting female mate choice include, for instance, male density, male-male competition (Cotton et al., 2006) and environmental factors hindering detection or discrimination of male sexual signals (e.g., Halfwerk et al., 2017; Cronin et al., 2019; Taylor et al., 2021; Wilgers et al., 2022). Background noise is an extrinsic factor that can limit female detection and discrimination of acoustic signals. To overcome this, males can use multimodal communication, such as a combination of acoustic and visual signals, to increase their chances of being detected and chosen by females (Rosenthal et al., 2004). Multimodal signals are considered more efficient than unimodal signals, as they are received through multiple sensory modalities (Partan and Marler, 2005). They may evolve through efficacy-based selection, improving the probability or intensity of receiver response in varying environmental conditions, including noise (Hebets and Papaj, 2005). Studies show that females in many species prefer multimodal over unimodal signals (Elias et al., 2006; Girard et al. 2015; Kozak and Uetz, 2019), but few have explored how background noise affects female mate choice in response to uni- and multimodal signals (e.g., Reichert and Ronacher, 2014).

In general, the interaction between intrinsic and extrinsic factors and the variation in conspicuity of different signals emitted by a prospective mate are expected to play a key role in modulating female mate choice. Consider a species in which males emit visual (v), acoustic (a), or multimodal (m) signals to attract females. In this example, the signal m is the most conspicuous to females because it stimulates two sensory modalities. Signal v is the least conspicuous because the receiver must be oriented toward the signaler to perceive the signal. Finally, the conspicuity of signal a is intermediate between m and v because it stimulates females but suffers from background noise interference (Figure 1a). When we introduce inter-individual variation in an intrinsic factor, such as female body condition, choosiness to different signals can be modified. The differential costs of mate sampling for females in good and poor condition should make the former choosier than the latter, as explained above. However, regardless of females' body condition, their choosiness should be higher for signal *m*, lower for *v*, and intermediate for *a* (Figure 1b). Similarly, mate choice can be modified by natural variation in an extrinsic factor, such as background noise. The conspicuity of the signal *m* and *a* is negatively affected by the background noise, decreasing females' response to them, regardless of their body condition. Given that the multimodal signal also includes a visual component, the negative effect of background noise on *m* should be lower than on signal *a*. Finally, because the signal *v* is not affected by background noise, females' response to them should not be affected (Figure 1c).

Here we used a male mimicking robot frog to test the influence of female body condition and environmental background noise on female mate choice in *Crossodactylus schmidti*, a diurnal frog that inhabits and reproduces in streams in the austral Neotropics (see 'Study species' below). We tested the following hypotheses: (1) given that signals from different sensory modalities vary in conspicuity (Endler 1992) and multimodal signals tend to be more conspicuous than their unimodal components (Bradbury and Vehrencamp, 1998; Partan and Marler, 2005), the female response should be higher to the multimodal (more conspicuous signal), intermediate to the acoustic, and lower to the visual signal (less conspicuous signal) (Figure 1a); (2) because the response to a sexual signal may be influenced by intrinsic factors (Cotton et al., 2006), the better the condition of the females, the choosier they should be, and the sequence of female choosiness in response to different signals should be: multimodal >

acoustic > visual, regardless of their body condition (Figure 1b); (3) because the conspicuity of the multimodal signal is usually higher than that of the acoustic signal alone (e.g., Rosenthal et al., 2004; Mitoyen et al., 2019), the negative effect of background noise on female response to the multimodal signal should be lower than to the acoustic signal, but the response to the visual signal should not be affected by the background noise (Figure 1c).

MATERIAL AND METHODS

Study area

The study was carried out in two streams in Turvo State Park (27°14′34.08″S, 53°57′13.74″W, 376 m a.s.l.), located in the municipality of Derrubadas, state of Rio Grande do Sul, southern Brazil. The park covers an area of nearly 17,500 ha and is one of the largest remnants of semideciduous forest in southern Brazil. The local climate is characterized as subtropical subhumid with a dry summer between December and March. The mean annual rainfall is 1,787 mm, the mean annual temperature is 18.8 °C and mean temperature of the coldest month is 13.3 °C (Maluf, 2000). In the area, several previous studies on the ecology and behavior of *Crossodactylus schmidti* have been conducted (e.g., Caldart et al., 2014, 2016a,b, 2022).

Study species

The diurnal Neotropical stream-dwelling frog *C. schmidti* is a suitable study system to test the hypotheses outlined here. Males compete for and defend territories containing rocks (signaling sites) and underwater chambers (oviposition sites) emitting visual, acoustic, and multimodal signals (Caldart et al., 2011, 2014, 2022). Males emit an audiovisual display composed of the simultaneous emission of calls and toe flags (Caldart et al., 2011, 2014), i.e., up-and-down movements performed with the toes, in which toes are lifted slowly from the substrate, showing the contrasting coloration between their ventral and dorsal parts (Hödl and Amézquita, 2001; Hartmann et al., 2005; see also Supplementary Videos in Appendix S1). The display is used in both in agonistic interactions with males and in courtship interactions (Caldart et al., 2014). An experimental study using a male mimicking robot frog has shown that toe flags emitted in association with aggressive calls appear to provide contextual information that modifies the receiver's response in territorial contests (Caldart et al., 2022). However, the role of toe flags associated with calls directed at females remains unknown.

Sexually mature individuals occur year-round (Caldart et al., 2019), and males are found in call and visual signaling activity from sunrise to sunset (Caldart et al., 2016b). Advertising males may emit the advertisement call and the aggressive call independently, with long intervals between the two calls, or may emit both calls sequentially, i.e., aggressive call followed by advertisement call (Caldart et al., 2011). Sequential aggressive-advertisement calls were described to other species of the family Hylodidae (e.g., Nascimento et al., 2005) and possibly compose a multiple signal, with the aggressive call serving to keep conspecific males away and the advertisement call serving to attract females (Caldart et al., 2011). High background noise levels caused by waterflow impair part of the multinote trilled advertisement call of males (Caldart et al., 2016a), which probably hampers sexual communication between males and females.

Courtship involves a female evaluation of signals emitted by the male. These signals include aggressive-advertisement calls directed to nearby males, visual signals including limb liftings and more frequently toe flags, and various multimodal signals (i.e., acoustic and visual) directed to the approaching female (Caldart et al., 2014). When a female is receptive, she moves toward the male and signals back using a low-amplitude call or visual signals, such as limb lifting, toe flagging, body jerking, and running-jumping display (Caldart et al., 2014). Before diving to the oviposition chamber, the female who has accepted a courting male interacts tactilely with him via an amplexus-like stimulus (Caldart et al., 2019; see also Supplementary Videos in Appendix S1).

Stimuli preparation and experimental procedure

We developed an electromechanical robot frog that simulates a *C. schmidti* male and programmed the robot to emit calls and toe flags, combined or in isolation. Then, we exposed the robot to females in the field to induce interactions. A general overview of the electromechanical robot, as well as films of the robot frog in action and the receivers' responses to it, are presented in Caldart et al. (2022).

To test our hypotheses, we programmed the robot to emit three types of stimuli: (1) acoustic (calls only), (2) visual (toe flags only), and (2) multimodal (calls and toe flags). The three types of stimuli had the same temporal structure, composed of an 8-min stimulus phase. The stimulus phase of the multimodal signal was composed of a train of 12 s of aggressive-advertisement call with a simultaneous toe flag in the middle of each call, followed by 28 s of silent interval. This sequence was repeated 12 times during the stimulus phase. In the case of the acoustic stimulus alone, the robot emitted aggressive-advertisement calls without toe flags. The acoustic stimulus consisted of a multiple call recorded from an average-sized male used in the original call description (Caldart et al., 2011), with temporal features modified in Adobe Audition to match population means and standardized at a sound pressure level of 70 dB (Caldart et al., 2011, 2016; see also Appendix S2). The exact moments of signal emission during the stimulus phase were the same for the three types of stimuli. Finally, in the case of the visual stimulus alone, the robot emitted toe flags without calls. The duration of the toe flag movement programmed in the robot was 0.4 s, which is equal to the average duration of the signal as reported in Caldart et al. (2014) and used in a previous experiment (Caldart et al., 2022).

We located and captured females in November and December 2017. Then we registered the snout-vent length (SVL, precision 0.01 mm) and body mass (precision 0.1 g) of the females and marked them with a temporary cotton waist belt around the pelvic region containing an individual color code. After the release of the females to their respective sites, we tied a degradable flag containing the individual code of the female in the vegetation right above the site where each individual was captured. Because females are territorial, we could locate the same females during the experiment to expose each of them to more than one type of stimulus in a repeated measure experimental design. One day after the marking procedure, we searched for marked females between 09:00 and 17:00 h. After finding a marked female, we observed the female for 5 min to ensure that they were active and positioned the robot at a viewing distance of 70 cm, at an angle of 30° relative to the focal female (as in Caldart et al., 2022). We then waited for 2 min for acclimatization and, if the focal female was not disturbed jumping in the water, we exposed her to one of the three experimental stimuli. We randomized the sequence of presentation of stimuli to each female to avoid the influence of the order of exposure of stimulus type on females' responses.

We recorded the entire trial for each focal female with a digital camcorder (Sony Handycam HDR-CX405). Immediately after the footage, we measured the background noise level (dB) 30 cm above the female site with a sound level meter (Instrutherm DEC 500; C weighting curve: 20–12,500 Hz, dB range: 35–130 dB). After finishing a trial, we either waited for at least 30 min (plus 2 min of acclimatization) before assigning another experimental stimulus to the same focal female—continuing the trial only if the female had stopped interacting with the robot—or moved the robot to another site and repeated the procedure with another female. We recorded 26 females, of which 19 were exposed to the three types of stimulus, 6 were exposed to at least two types of stimulus (i.e., acoustic and multimodal), and one was exposed to only one type of stimulus (i.e., acoustic). Thus, a total of 19 females were exposed to visual, 26 to the acoustic, and 25 to the multimodal stimulus.

Body condition was estimated as the residuals of an ordinary least square regression between $\log_{10}$-transformed$\log_{10}$-transformed body mass and $\log_{10}$-transformed SVL. The residual index has been extensively used to estimate condition in amphibians (reviewed in Brodeur et al., 2020), including a previous study with *C. schmidti* (Caldart et al., 2022). Positive residuals indicate that individuals have better body condition than individuals with negative residuals.

Statistical analyses

We investigated whether the stimulus type, female body condition, and background noise (predictor variables) affected female responses to the robot using model selection of generalized linear mixed models (GLMMs) or random-effect (frailty) Cox Proportional Hazards models (CPHs), depending on the type of response variable. In the GLMMs and CPHs, female identity was included as a random factor to control for repeated exposure of the same individual to different experimental stimuli. Moreover, the two continuous predictors (i.e., body condition and background noise) were standardized and centered to zero to produce comparable effect sizes (Schielzeth, 2010).

The response variables used in the GLMMs were: (1) probability of emission of acoustic response (binomial distribution of errors with a cloglog link function), (2) probability of emission of visual response (binomial distribution of errors and logit link-function), which included the limb lifting, toe flagging, body jerking, and running-jumping display (Caldart et al., 2014), and (3) emission rate of acoustic and visual signals (Poisson distribution of errors and log link function). The response variables used in the CHPs were: (4) latency to acoustic response, (5) latency for visual response, and (6) latency for moving toward the robot. Because some females did not respond during the stimulus phase, the latency data were right censored (1 = nonrespondent females, 2 = respondent females).

These six response variables above are related to female responsiveness to sexual signals emitted by the robot. Regarding the stimulus type, we predicted that females would show high probability and emission rate of acoustic and visual signals, as well as lower latency to respond to the multimodal stimulus, followed by the acoustic and visual stimuli, respectively. Regarding body condition, we predicted that this trait would be negatively related to the probability and emission rate of acoustic and visual signals and positively related to the latency of female response. Assuming that females in poor body condition will invest less in mates searching, they should be more responsive than females in good body condition to an average quality male, such as our robot whose body size, as well as to the emission of acoustic and visual signals corresponding to the average values of males in the population (see ′Stimuli preparation and experimental procedure' above). Finally, with respect to background noise, we predicted that this trait would be negatively related to the probability and emission rate of acoustic and visual signals, and also to the latency of female response when the robot is emitting multimodal and acoustic signals, but not visual signals. Moreover, female responsiveness is expected to be more affected by background noise when the robot is emitting acoustic signals when compared to multimodal signals because the latter is more conspicuous than the former.

For each response variable, our model selection procedure followed the steps described below:

(1) Fit the global model (response variable ~ stimulus type * body condition * background noise + (1 | ind)); notation using R language.

(2) Check the goodness-of-fit of the global model, i.e., retrieve the model conditional R^2. If the global model had a good fit ($R^2 > 0.5$), we proceeded with the analysis because the best-fitted model would also have a good fit (Symonds and Moussalli, 2011).

(3) Model all possible combinations of simpler models based on global model terms to explore the explanatory power of competing models. Twelve models (the global model plus 11 simpler models including a null model), all of them with clear biological meaning, were fitted for each response variable.

(4) Calculate the ΔAIC_c and the Akaike weight (w_i) of every model and classify the models using their ΔAIC_c, which is a modified version of the AIC recommended for small sample sizes (Symonds and Moussalli, 2011).

(5) Accept the model with the lowest ΔAIC_c value and the highest Akaike weight (w_i) as the best fitted model (Symonds and Moussalli, 2011).

(6) In cases in which there was more than one model with $\Delta AIC_c < 2$, select as the best approximating model the one with the highest Akaike weight (w_i). Moreover, we also used an average model approach, according to which we built a model composed of all the terms included in the models with $\Delta AIC_c < 2$. The coefficients of the average model are the average of the estimated coefficients in each of these models, weighted by the weight of evidence of each model (Burnham and Anderson 2002). The model average approach aimed to check if the estimates of the best ranked model (i.e., the one with the highest w_i) are qualitatively similar to the estimates of the average model.

(7) Make diagnostic plots and tests for the best ranked models ($\Delta AIC_c < 2$) because AIC is affected by overdispersion in the data (Symonds and Moussalli, 2011). For the GLMMs, we tested the model's goodness-of fit, the significance of the dispersion parameter, and the presence of zero inflation (when applicable) using the package *DHARMa* (Hartig, 2020). For CPHs, we checked the proportional hazards assumption using the package *survival* (Therneau 2020).

(8) If diagnostic plots and tests were fine, present the 95% confidence set of best-ranked models, i.e., models with cumulative Akaike weight ≤ 0.95, and the average model, when applicable (Burnham and Anderson, 2002).

GLMMs were built using the package *glmmTMB* (Brooks et al., 2017), and the CPH models were fitted using the package *survival* (Therneau, 2020). Complete results and diagnostics for all models are presented in Appendices S3-S5. All statistical analyses were performed in software R version 4.0.2 (R Core Team, 2020).

RESULTS

General patterns of female response to robot stimuli

Females exhibited three types of response to the robot: emission of acoustic signals (hereafter acoustic response), emission of visual signals (hereafter visual response), and movements toward the robot. The proportion of responsive females was higher to the multimodal stimulus, lower to the visual stimulus, and intermediate to the acoustic stimulus, regardless of the type of female response. When all types of female response are pooled, the general pattern remains qualitatively the same (Figure 2).

Effects of stimulus type, body condition, and background noise on the probability of female acoustic response

The best-ranked model to explain the probability of female acoustic response included the additive effect of stimulus type and body condition. This model was the only one with $\Delta AIC_c < 2$ (Table 1, Figure 3a) and had a high goodness-of-fit (conditional $R^2 = 0.83$). When compared to the visual stimulus, the acoustic stimulus induced an intermediate probability of response, while the multimodal stimulus induced the highest probability of response and the visual stimulus induced the lowest probability of response. The probability of female acoustic response decreased with female body condition (Figure 3a). Detailed results of the GLMM performed using model selection are presented in Appendix S3.

Effects of stimulus type, body condition, and background noise on the probability of female visual response

The best-ranked model to explain the probability of female visual response included the interaction between stimulus type and background noise. This model was the only one with $\Delta AIC_c < 2$ (Table 1, Figure 3b) and had a high goodness-of-fit (conditional $R^2 = 0.62$). The multimodal stimulus induced the highest probability of female visual response, the visual stimulus induced the lowest probability of female visual response, and the acoustic stimulus induced intermediate probability values. The effect of background noise on the probability of female visual response depended on the of stimulus type (Figure 3b). Specifically, the probability of female visual response to visual and multimodal stimuli decreased with increasing background noise, whereas the probability of female visual response to the acoustic stimulus increased with background noise. Detailed results of the GLMM performed using model selection are presented in Appendix S3.

Effects of stimulus type, body condition, and background noise on the emission rate of signals by females

The model to explain the emission rate of signals by females included the additive effect of stimulus type, body condition, and background noise, but the other two models that included interaction terms also had $\Delta AIC_c < 2.0$ (Table 1). However, our interpretation is based on the best ranked model (conditional $R^2 = 0.80$) because it has the highest Akaike weight and the lowest number of parameters. Furthermore, the best ranked model's estimates are qualitatively similar to the estimates of the average model's estimates (Figure S1 in Appendix S4), indicating that the inclusion of additional parameters through model averaging does not increase the explanatory power of the model.

The best-ranked model indicates that the three types of stimulus had a similar effect on the emission rate of signals. The emission rate of signals decreased with female body condition and increased with background noise. In both cases, the effect was stronger for the acoustic stimulus, weaker for the visual stimulus, and intermediate for the multimodal stimulus, although the confidence intervals of the estimates overlap (Figures 3c-d). Detailed results of all GLMMs performed using model selection are presented in Appendix S3.

Effects of stimulus type, body condition, and background noise on the latency to female responses

The best-ranked model to explain the latency to female acoustic response included only body condition, a predictor also present in the second best-ranked model, which includes the additive effect of background noise (Table 2, Figure 4a). Our interpretation of the results will be based on the best-ranked model because this model has an Akaike weight more than two times higher than the second model (Table 2) and the confidence interval of its parameter estimates does not overlap zero. Furthermore, in the average model, the background noise confidence interval overlaps zero, indicating that this variable does not add more explanatory power to the model (Table S1 in Appendix S4). Body condition affected female response, so that females in better body condition took longer to respond with acoustic signals after the onset of robot stimuli (Figure 4a).

The best-ranked model to explain the latency of the visual response included the additive effects of body condition and background noise, predictors that were also present in four of the five best ranked models (Table 2, Figure 4b). However, our interpretation of the results will be based on the best-ranked model because this model has an Akaike weight higher than the other models (Table 2) and the confidence interval of the parameters’ estimates does not overlap zero. Furthermore, contrary to the best-ranked model, the confidence interval of all parameters in the average model overlaps zero, indicating that the inclusion of additional parameters through model averaging does not increase the explanatory power of the model (Table S1 in Appendix S4). Females in better body condition and in sites with more background noise took longer to respond with visual signals after the onset of robot stimuli (Figures 4b-c).

The best-ranked model to explain the latency to moving toward the robot included the additive effects of stimulus type, body condition, and background noise (Table 2). Among the four best ranked models, stimulus type appeared in all of them, body condition in three of them, and background noise in two of them (Table 2). Our interpretation of the results will be based on the best ranked model because this model has an Akaike weight slightly higher than the other models (Table 2), and the confidence interval of the parameters’ estimates does not overlap zero. As in the previous analyses, the confidence interval of body condition and background noise in the average model overlaps zero, indicating that the inclusion of additional parameters through model averaging does not increase the explanatory power of the model (Table S1 in Appendix S4). Females in better body condition and in sites with more background noise took longer to move toward the robot (Figure 4c-d). Finally, the stimulus type affected the latency of female movement toward the robot, since for all types of stimulus more than 50% of the females moved toward the robot (Figure 5c). Females took longer to move toward the robot when the robot emitted the visual stimulus (median latency = 364 s) but moved much faster toward the robot when it emitted the multimodal stimulus (median latency = 50 s) or the acoustic stimulus (median latency = 58 s). Detailed results of all CPH models performed using model selection on latency data are presented in Appendix S5.

DISCUSSION

To test hypotheses on how body condition and background noise modify females' responsiveness to signals of varying conspicuity, we innovate by presenting a male mimicking robot frog to females of the diurnal stream-dwelling frog *Crossodactylus schmidti*. Our main results are: (a) females are more responsive to the multimodal signal than to visual and acoustic signals, (b) females in good body condition are less responsive than females in poor body condition, and (c) females at noisier sites exhibit decreased probability of responding with a visual signal (except in response to the acoustic stimulus), emit signals at a higher rate, and take more time to signaling or moving towards the robot. In what follows we explain how these results support predictions about the effects of signal conspicuity and intrinsic and extrinsic factors on female mate choice (Figure 1) and contribute to understanding how mate choice is shaped by the interplay between signal conspicuity, female body condition, and background noise.

For any type of response we evaluated, females were more responsive to the multimodal stimulus, followed by the visual and acoustic stimuli, respectively. This finding supports our hypothesis that signal conspicuity influences female response to sexual signals emitted by males and confirms the prediction that the sequence of signal conspicuity is multimodal > acoustic > visual. Although there are several studies showing that females are more responsive to multimodal signals compared with unimodal signals (e.g., Elias et al., 2006; Estramil et al., 2014; Girard et al. 2015), only a few experimental studies provide quantitative support for this sequence among visually and acoustically oriented species (e.g., Reichert and Höbel, 2015; Laird et al., 2016). Given that the content of a signal cannot be perceived and processed if it is not properly detected (Wilgers et al., 2022), multimodal signals can contribute to more informed decision-making during mate choice when compared with unimodal signals. In fact, multimodal signals are believed to be more advantageous because they convey more information per unit time, increasing opportunities for effective communication (Rojas et al., 2018; Kabir and Thaker, 2021). Thus, we suggest that females of *C. schmidti* are more responsive to the multimodal signal because it is more easily detected, and also carries additional information about male signalers. Our suggestion implies content-based and efficacy-based selection on the evolution of multimodal signals mediated by female response (Hebets and Papaj, 2005). We stress that we do not have information on what specific information toe flags accompanying calls carries during mating interactions in the study species. However, our results indicate that the integration of multiple sensory modalities in male signals enhances females' response.

Females in better body condition were less responsive to male signals, exhibiting lower probability of acoustic response, emitting signals at a lower rate, and taking more time to emit signals or move towards the robot. Female acoustic response, particularly, decreased with body condition in the expected sequence of signal conspicuity (multimodal > acoustic > visual), further supporting the hypothesis that signal conspicuity influence female-male communication during sexual interactions. The consistent pattern across different types of female response indicates a prevalent negative effect of body condition on female responsiveness (a proxy of choosiness, see Edward, 2015). Our findings are qualitatively similar to previous empirical studies with a wide variety of other taxa showing that choosiness is a condition-dependent trait in females (e.g., Milinski and Bakker, 1992; Hunt et al., 2005; Cotton et al., 2006;

Wilgers and Hebets, 2012; Lerch et al., 2013; Judge et al., 2014; but see Dougherty, 2023). In the case of *C. schmidti*, females in good body condition can invest more time and energy in mate sampling and mate evaluation, leading to more selective responses, which ultimately increase their chances of finding a high quality male. By signaling less frequently, females in better condition demonstrate higher selectivity for potential mates, which possibly helps them avoid mating with lower-quality males and increase their chances of securing a high-quality mate.

Females at noisier sites exhibited response patterns that suggest different mechanisms of noise interference on mate choice. With increasing noise, females exhibited a decreased probability of responding with a visual signal to both visual and multimodal stimuli emitted by the robot frog. This pattern can be explained by cross-modal sensory interference effects (e.g., Stoffels et al., 1985), such as when a sensory input in one modality inhibits perception or attention to stimuli in another modality (e.g., perceptual suppression in Ide and Hidaka, 2013). This effect is known to humans, in which acoustic noise degrades visual orientation (Hidaka and Ide, 2015). Cross-modal sensory interference has also been reported in Caribbean hermit crabs, in which anthropogenic acoustic noise disrupts response to visual predatory cues (Chan et al., 2010). More recently, a laboratory experiment with an anuran species showed that acoustic noise disrupts female responses to visual and audiovisual stimuli during mate choice (Zhu et al., 2022). Our findings obtained under natural conditions suggest the presence of cross-modal sensory interference in an anuran that inhabits streams where background noise is intense (Caldart et al., 2016a). With increasing stream-generated noise, females of *C. schmidti* appear to undergo sensory suppression, hindering their response to visual and multimodal stimuli. Since both stimuli involve the visual component of toe flagging, noise-induced suppression may impede females from extracting important information from these signals, leading to a reduced responsiveness to them.

When exposed to the acoustic stimulus, females exhibited a higher probability of visual response as the noise increased. A possible explanation for this seemingly paradoxical result is that in anurans from lothic habitats, females have adapted their sensory tuning to match the frequency range of male calls and filter out background noise (Brumm and Slabbekoorn, 2005). However, we argue that females of *C. schmidti* probably do not have such auditory adaptation because background noise negatively affects their responses. Moreover, the background noise in the studied site partially masks the multinote advertisement calls of males (Caldart et al., 2016a). Therefore, we consider an alternative explanation for the higher responsiveness to acoustic stimuli with increasing noise levels: females struggle to receive and interpret acoustic signals in noisy conditions, and increase their visual responses and emit signals at a higher rate to elicit more signaling from potential mates. Thus, heightened visual response of females at noisier sites may be a strategy to overcome the challenges of receiving acoustic signals in a noisy environment. The main implication of this strategy is that females in noisy environments need to allocate more time and energy to signaling in order to evaluate the quality of potential mates, which may also explain why females in poor body condition are less choosy than females in good body condition.

Females at noisier sites also took more time to respond with visual signals and to move towards the robot, results that further indicate that the background noise influences female mate choice. When exposed to high levels of background noise, females may need more time to make an informed decision about male quality before responding because they are not receiving clear or sufficient information from the signaler (e.g., due to auditory masking) or because their sensory system is experiencing reduced sensitivity (e.g., due to cross-modal sensory interference). Consequently, if noise interference makes signals more difficult to detect via cross-modal sensory interference or auditory masking, as our results suggest, females in noisier sites may require more time to gather sufficient information from the signaler and decide to respond or approach it. A recent study on the field cricket *Gryllus bimaculatus* found that females exposed to anthropogenic noise took longer to approach and mate with males, suggesting that noise interfered with their ability to make informed decisions about mate quality (Bent et al., 2021). The delayed response was attributed to the need for additional processing time in the presence of noise.

In conclusion, the results of our field experiment using a robot frog highlight the importance of signal conspicuity in shaping female mate choice, with females being more responsive to the multimodal stimulus compared to the unimodal stimuli. This underscores the importance of integrating multiple sensory modalities into male signals to improve detectability and elicit stronger female responses. Our results also reveal the role of female body condition in influencing mate choice. The consistent patterns observed in different females' behavioral responses indicate the strong negative effect of body condition on female mate choice. A better body condition was consistently associated with a lower probability of response, a lower signaling rate, and a longer time to respond to the signals emitted by the robot frog. This finding supports the notion that female mate choice in a condition dependent trait, so that females in good body condition are choosier than females in poor body condition. Additionally, we found that background noise has important effects on females' behavioral responses. Females at noisier sites were less responsive overall, except in response to the acoustic stimulus, emitting signals at a higher rate and requiring more time to respond. This finding can be attributed to different mechanisms of noise interference which deserve further investigation: 1) cross-modal sensory interference, as females at noisier sites decreased response to stimulus presenting the visual stimulus, suggesting that background noise hampers the perception and processing of visual signals; and 2) auditory masking, as females struggled to receive and interpret the acoustic signal in noisy conditions and increased their response in order to elicit more signaling from males. Finally, our study emphasizes that signal conspicuity, female body condition, and noise levels shape female-male sexual interactions, revealing the complexity and context-dependent nature of the mechanisms underlying female mate choice.

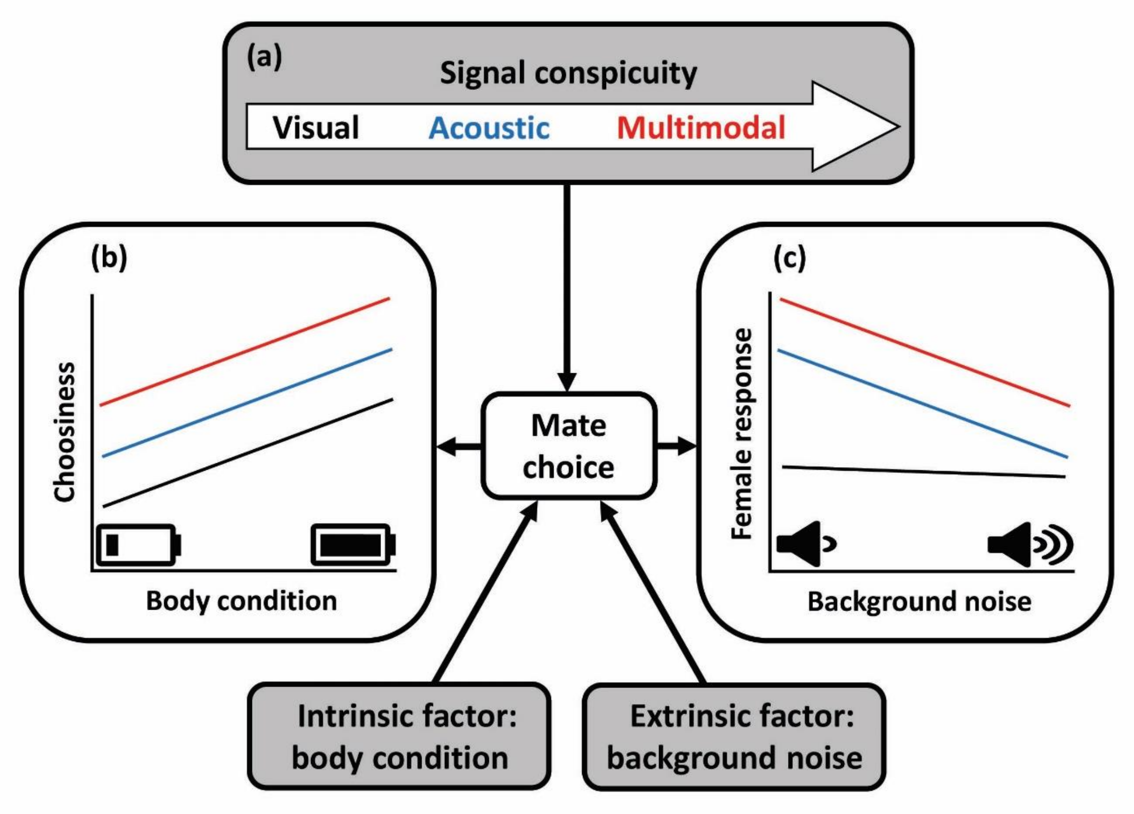

Figure 1

Hypotheses tested in this study: (a) given that signals from different sensory modalities vary in conspicuity, females' response should be higher to the multimodal (more conspicuous), lower to the visual signal (less conspicuous), and intermediate to the acoustic; (b) because the response to a signal may be influenced by the receiver's body condition, with high-quality females being choosier than low-quality females, the response to all signals should decrease as female body condition increases, although differences in the responses between signals are maintained by variation in signal conspicuity; (c) because the response to an acoustic signal may be impaired by background noise, females' response to the acoustic and multimodal signal should increase as the background noise decreases, and the probability of female response should be higher to the multimodal signal across the noise gradient; response to the visual signal is unaltered because this signal is not affect by background noise.

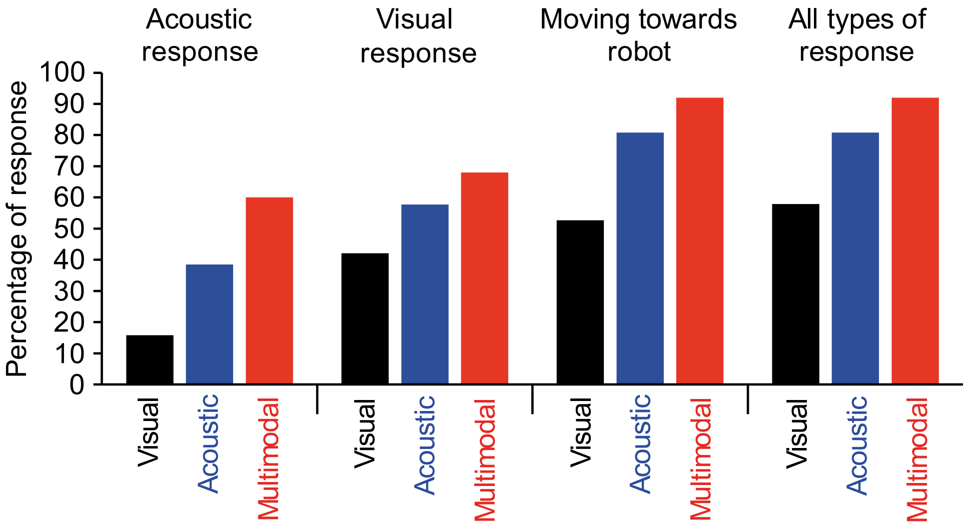

Figure 2

Percentage of females of the frog *Crossodactylus schmidti* that responded with acoustic signaling, visual signaling, or moving toward the male mimicking robot frog after the onset of visual (*N* = 19, black bars), acoustic (*N* = 26, blue bars), and multimodal (*N* = 25, red bars) stimuli emitted by the robot.

Table 1

Results of the model selection of generalized linear-mixed models used to investigate the effect of type of stimulus (acoustic, visual, and multimodal), body condition, and background noise on the probability of acoustic and visual response, as well as on the emission rate of signals by *Crossodactylus schmidti* females to a male mimicking robot frog. For each response variable, the list of models shown represent the 95% confidence set of best-ranked models, i.e., models with cumulative Akaike weight (w_i) ≤ 0.95.

Response variable	**Rank**	**Candidate model**	k	**AIC_c**	**ΔAIC_c**	w_i
Probability of acoustic response	1	**stimulus type + condition**	**5**	**77.4**	**0.0**	**0.512**
	2	stimulus type	4	79.6	2.3	0.164
	3	stimulus type + condition + noise	6	79.7	2.3	0.161
	4	stimulus type * condition	7	80.5	3.2	0.106
Probability of visual response	1	**stimulus type * noise**	**7**	**94.4**	**0.0**	**0.564**
	2	noise	3	98.5	4.1	0.072
	3	stimulus type * condition	7	98.7	4.3	0.067
	4	null	2	98.9	4.5	0.059
	5	stimulus type + noise	5	99.3	4.9	0.048
	6	stimulus type	4	99.7	5.3	0.041
	7	noise + condition	4	99.7	5.3	0.040
	8	condition	3	100.4	6.0	0.028
	9	stimulus type + condition + noise	6	100.6	6.2	0.025
Emission rate of signals	1	**stimulus type + condition + noise**	**6**	**273.7**	**0.0**	**0.381**
	2	**stimulus type * condition * noise**	**13**	**275.0**	**1.3**	**0.195**
	3	**stimulus type * condition**	**7**	**275.3**	**1.6**	**0.170**
	4	stimulus type + condition	5	275.8	2.1	0.131
	5	stimulus type * noise	7	277.9	4.2	0.047

All models include female identity as random effect. Models are ranked by increasing order of their ΔAIC_c values. The best models to fit the observed data ($\Delta\text{AIC}_c < 2.0$) are indicated in boldface. k = number of parameters, ΔAIC_c = difference between the AIC_c value of each model and the AIC_c value of the best-ranked model, and w_i = AIC_c weight of each model. The symbol + indicates an additive effect between variables, and the symbol * indicates an interaction between variables.

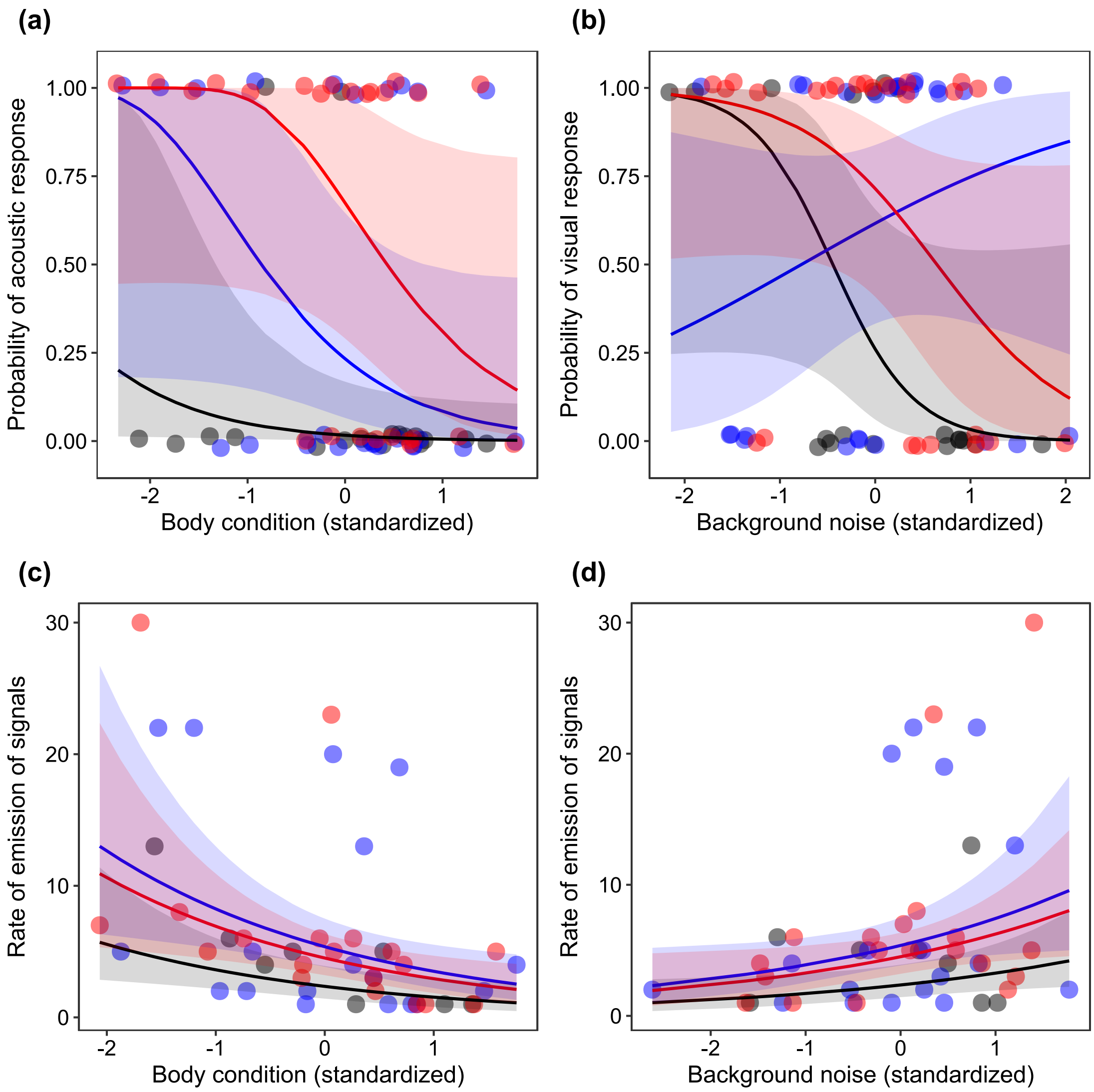

Figure 3

Effects of type of stimulus, female body condition, and background noise on the probability of response and emission rate of signals by *Crossodactylus schmidti* females to a male mimicking robot frog. Stimulus-specific relationships between: (a) female body condition and probability of acoustic response, (b) background noise and probability of visual response, (c) body condition and emission rate of signals, and (d) background noise and emission rate of signals. In all cases the stimulus emitted by a male mimicking robot frog is represented in different colors: visual = black lines and dots; acoustic = blue lines and dots; multimodal = red lines and dots. Tendency lines shown here for each response variable are based on the best-ranked models (Table 1).

Table 2

Results of the model selection on random-effect (frailty) Cox Proportional Hazards used to investigate the effect of type of stimulus (acoustic, visual, and multimodal), body condition, and background noise on the latency to acoustic response, latency to visual response, and latency to moving toward robot by *Crossodactylus schmidti* females to a male mimicking robot frog. For each response variable, the list of models shown represent the 95% confidence set of best-ranked models, i.e., models with cumulative Akaike weight (w_i) ≤ 0.95.

Response variable	**Rank**	**Candidate model**	**AICc**	**ΔAICc**	***k***	***wi***
Latency to acoustic response	1	**condition**	**213.8**	**0.0**	**5.3**	**0.630**
	2	**noise + condition**	**215.7**	**1.8**	**5.8**	**0.250**
Latency to visual response	1	**noise + condition**	**292.5**	**0.0**	**8.6**	**0.292**
	2	**noise * condition**	**293.3**	**0.8**	**8.9**	**0.191**
	3	**stimulus type + condition + noise**	**293.6**	**1.1**	**9**	**0.167**
	4	**noise**	**293.8**	**1.3**	**9.5**	**0.153**
	5	**condition**	**294.3**	**1.9**	**10.1**	**0.115**
Latency to moving toward robot	1	**stimulus type + condition + noise**	**387.8**	**0.0**	**10.2**	**0.297**
	2	**stimulus type * condition**	**388.0**	**0.2**	**17.9**	**0.274**
	3	**stimulus type + noise**	**388.8**	**1.0**	**10.9**	**0.181**
	4	**stimulus type + condition**	**389.4**	**1.6**	**12**	**0.134**

All models include female identity as random effect. Models are ranked by increasing order of their ΔAIC_c values. The best models to fit the observed data ($\Delta AIC_c < 2.0$) are indicated in boldface. k = number of parameters, ΔAIC_c = difference between the AIC_c value of each model and the AIC_c value of the best-ranked model, and w_i = AIC_c weight of each model. The symbol + indicates an additive effect between variables, and the symbol * indicates an interaction between variables.

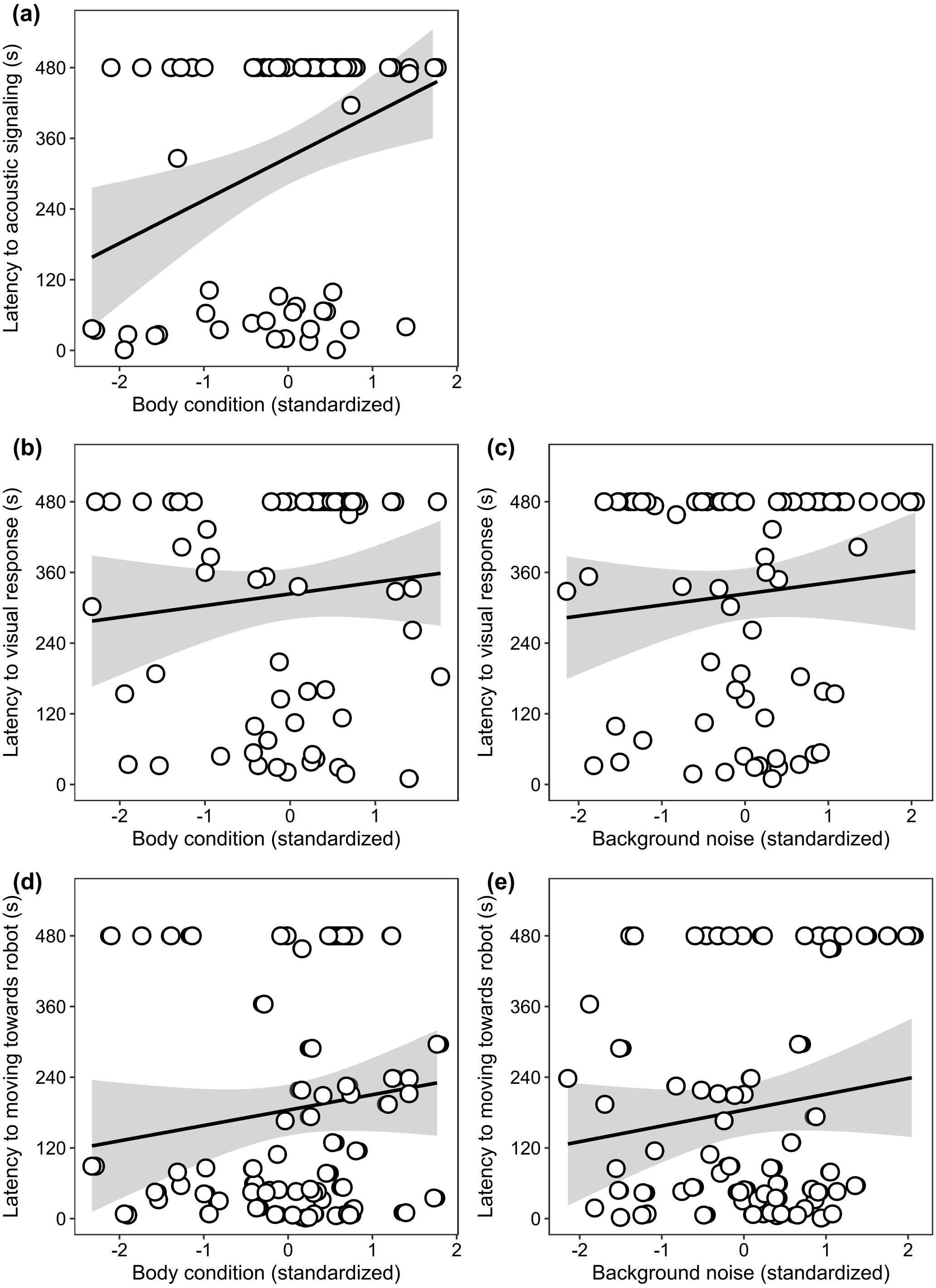

Figure 4

Effects of body condition on the latency of *Crossodactylus schmidti* females to respond to the stimulus emitted by the male mimicking robot frog. Overall relationship between: (a) female body condition and latency to acoustic response, (b) female body condition and latency to visual response, (c) background noise and latency to acoustic response, (d) female body condition and latency to moving towards robot, and (e) background noise and latency to moving towards robot. Tendency lines shown here for each response variable are based on the best-ranked models (Table 2).

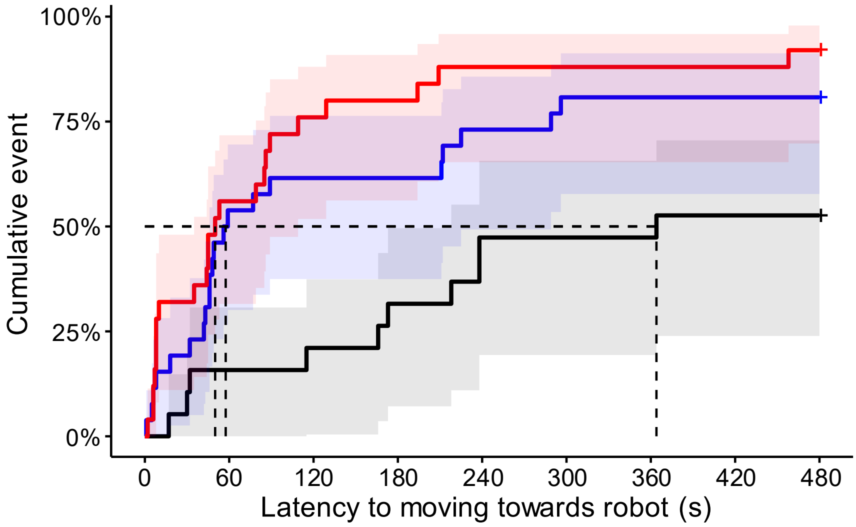

Figure 5

Cumulative event probability curves for the latency of *Crossodactylus schmidti* females to moving towards the robot frog in response to visual (black lines), acoustic (blue lines), and multimodal (red lines) stimuli emitted by a male mimicking robot frog. A vertical rise in the curves indicates that a response occurred at that time. Colored areas indicate the 95% confidence interval for each curve. Dashed lines indicate the median latency to respond to each experimental stimulus.

ACKNOWLEDGMENTS

We thank Tiago Theis, Álvaro Mainardi, Lívia Miron, Samanta Iop, Maiquel Elsenbach, and Maicon Elsenbach for helping in fieldwork, Sonia Cechin for lending field equipment, and Eileen Hebets for suggestions on the manuscript.

CONFLICT OF INTEREST

The authors declare that they have no conflicts of interest.

AUTHOR'S CONTRIBUTIONS

VMC and GM conceived the study and designed methodology, VMC and MBS built the robot, VMC collected and analyzed the data, VMC wrote the first version of the manuscript. All authors revised the statistical analyses and multiple versions of the manuscript.

DATA AVAILABILITY STATEMENT

Data will be available at Dryad Digital Repository upon manuscript acceptance.

ETHICAL NOTE

This project was authorized by the license #21/2016 and authorization #173/2016 for temporary marking of individuals, provided by the Divisão de Unidades de Conservação da Secretaria do Ambiente e Desenvolvimento Sustentável do Estado do Rio Grande do Sul. No individual was collected or held in captivity during this study.

REFERENCES

Amorim, M. C. P., S. S. Pedroso, M. Bolgan, J. M. Jordão, M. Caiano, and P. J. Fonseca. 2013. Painted gobies sing their quality out loud: acoustic rather than visual signals advertise male quality and contribute to mating success. Functional Ecology 27:289–298.

Andersson, M. 1994. Sexual selection. Princeton University Press, Princeton, NJ.

Bent, A. M., T. C. Ings, and S. L. Mowles. 2021. Anthropogenic noise disrupts mate choice behaviors in female *Gryllus bimaculatus*. Behavioral Ecology 32:201–210.

Bonduriansky, R. 2001. The evolution of male mate choice in insects: a synthesis of ideas and evidence. Biological Reviews 76:305–339.

Bradbury, J. W., and S. L. Vehrencamp. 1998. Principles of animal communication. Sinauer, Sunderland, MA.

Brooks, M. E., K. Kristensen, K. J. Benthem, A. Magnusson, C. W. Berg, A. Nielsen, H. J. Skaug, M. Maechler, and B. M. Bolker. 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. The R Journal 9:378–400.

Brumm, H., and H. Slabbekoorn. 2005. Acoustic communication in noise. Advances in the Study of Behavior 35:151–209.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer, Berlin, Germany.

Caldart, V. M., S. Iop, and S. Z. Cechin. 2011. Vocalizations of Crossodactylus schmidti Gallardo, 1961 (Anura, Hylodidae): advertisement call and aggressive call. North-Western Journal of Zoology 7:118–124.

Caldart, V. M., S. Iop, and S. Z. Cechin. 2014. Social interactions in a neotropical stream frog reveal a complex repertoire of visual signals and the use of multimodal communication. Behaviour 151: 19–739.

Caldart, V. M., S. Iop, R. Lingnau, and S. Z. Cechin. 2016a. Communication in a noisy environment: short-term acoustic adjustments and the underlying acoustic niche of a Neotropical stream-breeding frog. Acta Ethologica 19:151–162.

Caldart, V. M., S. Iop, R. Lingnau, and S. Z. Cechin. 2016b. Calling activity of a stream-breeding frog from the austral Neotropics: temporal patterns of activity and the role of environmental factors. Herpetologica 72:90–97.

Caldart, V. M., L. Loebens, A. J. C. Brum, L. Bataioli, and S. Z. Cechin. 2019. Reproductive cycle, size and age at sexual maturity, and sexual dimorphism in the stream-breeding frog *Crossodactylus schmidti* (Hylodidae). South American Journal of Herpetology 14:1–11.

Caldart, V. M., M. B. dos Santos, and G. Machado. 2022. Function of a multimodal signal: A multiple hypothesis test using a robot frog. Journal of Animal Ecology 91:701–714.

Chan, A. A. Y. H., P. Giraldo-Perez, S. Smith, and D. T. Blumstein. 2010. Anthropogenic noise affects risk assessment and attention: the distracted prey hypothesis. Biology Letters 6:458–461.

Cotton, S., J. Small, and A. Pomiankowski. 2006. Sexual selection and condition-dependent mate preferences. Current Biology 16:R755–R765.

Cronin, A. D., M. J. Ryan, R. A. Page, K. L. Hunter, and R. C. Taylor. 2019. Environmental heterogeneity alters mate choice behavior for multimodal signals. Behavioral Ecology and Sociobiology 73:1–10.

Dougherty, L. R. 2023. The effect of individual state on the strength of mate choice in females and males. Behavioral Ecology 34:197-209.

Edward, D. A., and T. Chapman. 2011. The evolution and significance of male mate choice. Trends in Ecology and Evolution 26:647–654.

Edward, D. A. 2014. The description of mate choice. Behavioral Ecology 26: 301–310.

Elias, D. O., E. A. Hebets, and R. R. Hoy. 2006. Female preference for complex/novel signals in a spider. Behavioral Ecology 17:765–771.

Endler, J. A. 1992. Signals, signal conditions, and the direction of evolution. The American Naturalist 139:S125–S153.

Estramil, N., N. Bouton, M. N. Verzijden, K. Hofker, K. Riebel, and H. Slabbekoorn. 2014. Cichlids respond to conspecific sounds but females exhibit no phonotaxis without the presence of live males. Ecology of Freshwater Fish 23:305–312.

Girard, M. B., D. O. Elias, and M. M. Kasumovic. 2015. Female preference for multi-modal courtship: multiple signals are important for male mating success in peacock spiders. Proceedings of the Royal Society B 282: 20152222.

Gomez, D., C. Richardson, T. Lengagne, S. Plenet, P. Joly, and M. Théry. 2009. The role of nocturnal vision in mate choice: females prefer conspicuous males in the European tree frog (*Hyla arborea*). Proceedings of the Royal Society B 276:2351–2358.

Halfwerk, W., J. A. Smit, H. Loning, A. M. Lea, I. Geipel, J. Ellers, and M. J. Ryan. 2017. Environmental conditions limit attractiveness of a complex sexual signal in the túngara frog. Nature Communications 8:1891.

Hartig, F. 2020. DHARMa: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models. R package version 0.2.7. Available at: https://CRAN.R-project.org/package=DHARMa.

Hebets, E. A., and D. R. Papaj. 2005. Complex signal function: developing a framework of testable hypotheses. Behavioral Ecology and Sociobiology 57:197–214.

Hunt, J., R. Brooks, and M. D. Jennions. 2005. Female mate choice as a condition-dependent life-history trait. The American Naturalist 166:78–92.

Jennions, M. D., and M. Petrie. 1997. Variation in mate choice and mating preferences: a review of causes and consequences. Biological Reviews 72: 283–327.

Judge, K. A., J. J. Ting, and D. T. Gwynne. 2014. Condition dependence of female choosiness in a field cricket. Journal of Evolutionary Biology 27:2529–2540.

Kabir, M. S., and M. Thaker. 2021. Does the addition of a new signaling trait enhance receiver responses in diurnal geckos? Behavioural Processes 184:104322.

Kozak, E. C., and G. W. Uetz. 2019. Male courtship signal modality and female mate preference in the wolf spider *Schizocosa ocreata*: results of digital multimodal playback studies. Current Zoology 65:705–711.

Laird, K. L., P. Clements, K. L. Hunter, and R. C. Taylor. 2016. Multimodal signaling improves mating success in the green tree frog (*Hyla cinerea*), but may not help small males. Behavioral Ecology and Sociobiology 70:1517–1525.

Lerch, A., L. Rat-Fischer, and L. Nagle. 2013. Condition-dependent choosiness for highly attractive songs in female canaries. Ethology 119:58–65.

Milinski, M., and T. C. M. Bakker. 1992. Costs influence sequential mate choice in sticklebacks, *Gasterosteus aculeatus*. Proceedings of the Royal Society B 250:229–233.

Mitoyen, C., C. Quigley, and L. Fusani. 2019. Evolution and function of multimodal courtship displays. Ethology 125:503–515.

Nascimento, L. B., C. A. Cruz, and R. N. Feio. 2005. A new species of diurnal frog in the genus *Crossodactylus* Duméril and Bibron, 1841 (Anura, Leptodactylidae) from southeastern Brazil. Amphibia-Reptilia 26:497–505.

Partan, S., and P. Marler. 2005. Issues in the classification of multimodal communication signals. The American Naturalist 166:231–245.

Reichert, M. S., and G. Höbel. 2015. Modality interactions alter the shape of acoustic mate preference functions in gray treefrogs. Evolution 69:2384–2398.

Reichert, M. S., and B. Ronacher. 2015. Noise affects the shape of female preference functions for acoustic signals. Evolution 69:381–394.

Richards, S. A. 2005. Testing ecological theory using the information theoretic approach: examples and cautionary results. Ecology 86:2805–2814.

Rojas, B., E. Burdfield-Steel, C. De Pasqual, S. Gordon, L. Hernández, J. Mappes, O. Nokelainen, K. Rönkä, and C. Lindstedt. 2018. Multimodal aposematic signals and their emerging role in mate attraction. Frontiers in Ecology and Evolution 6:93.

Rosenthal, G. G., A. S. Rand, and M. J. Ryan. 2004. The vocal sac as a visual cue in anuran communication: an experimental analysis using video playback. Animal Behaviour 68:55–58.

Rowe, L., and D. Houle. 1996. The lek paradox and the capture of genetic variance by condition-dependent traits. Proceedings of the Royal Society B 263:1415–1421.

Symonds, M. R., and A. Moussalli. 2011. A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. Behavioral Ecology and Sociobiology 65:13–21.

Stoffels, E. J., M. W. Van der Molen, and P. J. G. Keuss. 1985. Intersensory facilitation and inhibition: Immediate arousal and location effects of auditory noise on visual choice reaction time. Acta Psychologica 58:45–62.

Taylor, R. C., K. O. Wilhite, R. J. Ludovici, K. M. Mitchell, W. Halfwerk, R. A. Page, M. J. Ryan, and K. L. Hunter. 2021. Complex sensory environments alter mate choice outcomes. Journal of Experimental Biology 224: jeb233288.

Therneau, T. 2020. A package for survival analysis in R. R package version 3.2-7. https://CRAN.R-project.org/package=survival

Uetz, G. W., J. A. Roberts, and P. W. Taylor. 2009. Multimodal communication and mate choice in wolf spiders: female response to multimodal versus unimodal signals. Animal Behaviour 78:299–305.

Vélez, A., J. J. Schwartz, and M. A. Bee. 2013. Anuran Acoustic Signal Perception in Noisy Environments. Pages 133–185 in H. Brumm, ed. Animal Communication and Noise. Animal Signals and Communication. Vol. 2. Springer, Berlin.

Wilgers, D. J., J. C. Watts, and E. A. Hebets. 2022. Habitat complexity and complex signal function – exploring the role of ornamentation. Behavioral Ecology 33:307–317.

Wilgers, D. J., and E. A. Hebets. 2012. Age-related female mating decisions are condition dependent in wolf spiders. Behavioral Ecology and Sociobiology 66:29–38.

Zhu, B., H. Zhang, Q. Chen, Q. He, X. Zhao, X. Sun, T. Wang, J. Wang, and Cui J. 2022. Noise affects mate choice based on visual information via cross-sensory interference. Environmental Pollution 308:119680.