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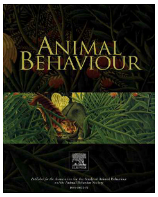

Consistent decisions of a predator facing potentially poisonous prey

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Decision making has important fitness consequences in domains as varied as foraging, mating and predator avoidance. In noisy ecosystems, animals often inform their decisions via information streams that may span sensory modalities. Despite theoretical predictions, we have little understanding of whether attending to multiple cues enhances decision-making performance or reduces it by creating cognitive overload. The predatory fringe-lipped bat, *Trachops cirrhosus*, hunts by eavesdropping on auditory prey cues, but it utilizes information from other sensory modalities when challenged in the laboratory and rapidly adopts new hunting behaviours through social learning. When hunting frogs, it uses their calls to identify palatable species. Túngara frog, *Engystomops pustulosus*, males court females with a multimodal display: their calls (auditory) and the simultaneously inflating vocal sac (visual) create water ripples (seismic). Here we evaluated decision making in fringe-lipped bats attending to ambiguous stimuli with and without additional cues. We quantified foraging decisions in response to synthesized hybrid calls spanning a gradient from calls of the palatable túngara frog to those of a poisonous toad. Hybrid calls were presented to bats in silence and with additional stimuli: social cues (conspecific chewing noises), environmental noise (anuran chorus) and additional cues associated with target frog calls (vocal sac motion and water ripples). We predicted (1) social and target cues would make hybrid calls more attractive as a potential food source and (2) decision making would be slower in the presence of noise. Counter to expectation, bats maintained highly consistent responses to hybrid stimuli regardless of treatment, supporting neither the enhanced performance hypothesis nor the cognitive overload hypothesis on decision making. We observed flexibility in minimum approach thresholds, however. Bats showed greater exploratory and risk-taking behaviour when given access to information in the form of target cues in noise. Our results elucidate how cognitively complex animals deal with information complexity in varying decision-making contexts.

Decision making has important fitness consequences in domains as varied as foraging, mating, habitat selection and predator avoidance. To make adaptive decisions, animals need sensory information. Uncovering how animals utilize sensory information for decision making remains fundamental to our understanding of behavioural ecology (Stevens, 2013).

When foraging, predators have access to different types of information. They can detect and localize their prey by means of the numerous incidental cues generated by prey, such as the visual and acoustic cues produced during movement (Konishi, 1973). Some predators are also able to exploit the communication systems that prey use for conspecific audiences, which often involve elaborate and conspicuous sensory signals for courtship (Bernal & Page, 2023; White et al., 2022; Zuk & Kolluru, 1998). Predator pressure from eavesdropping enemies can drive prey signalling behaviour, resulting in shifts in signal structure, the timing of signal production, or whether animals signal at all (Bernal & Page, 2023). Finally, many predators have access to socially acquired information. In interacting with knowledgeable conspecifics, naïve animals can find profitable feeding areas or learn new foraging strategies, such as associating a specific sensory cue with food (Clarin et al., 2014; Gaudet & Fenton, 1984; Jones et al., 2013; Page & Ryan, 2006; Patriquin & Ratcliffe, 2023; Ratcliffe & ter Hofstede, 2005; Rose, Kolar, Tschapka, & Knörnschild, 2016; Wilkinson, 1992).

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All types of information can be obscured by noise (Wiley, 2015). Noise refers to any sensory input that hinders an animal's perception of the signal, independent of the sensory domain. Acoustic noise is widespread and can disrupt behaviour through masking, distraction or misleading (Clark & Dukas, 2003; Gomes & Goerlitz, 2020). Masking occurs when noise overlaps in frequency with important signals or cues, thus impairing the detection or interpretation of the signal (Clark et al., 2009; Fay, 1988; Gomes et al., 2016; Tanner, 1958). Distraction is not limited to frequencies that overlap with the signal, as it occurs when noise competes for the attention of the receiver (Chan et al., 2010). Misleading occurs when noise is interpreted as something that it is not; i.e. a mechanism similar to a false alarm (Wiley, 2013) or a sensory trap (Christy, 1995; West-Eberhard, 1984). To overcome the hindering effects of noise, animals can recruit additional information streams, which can span sensory modalities (Gomes et al., 2016).

Most events in nature create disturbances that animals perceive through multiple information streams (Munoz & Blumstein, 2012). An approaching predator, for example, might generate cues in the visual, olfactory, acoustic and vibratory modalities. Furthermore, many species use more than one mode of signalling to effectively communicate, such as vocalizations and facial expressions in primates (Fröhlich & van Schaik, 2018). Multicomponent signals are often advantageous since more information should increase an animal's ability to detect important events and make informed decisions about them (Higham & Hebets, 2013; Kulahci et al., 2008; Rowe & Halpin, 2013; VanderSal & Hebets, 2007). We refer to this as the enhanced performance hypothesis. An example for this phenomenon is cross-modal facilitation (Keefe et al., 2021), a process whereby sensory performance in one modality is improved by stimulation in another modality, or performance that is otherwise abolished in the presence of noise is rescued through the use of multimodal (or multicomponent) information, e.g. improved understanding of speech in noisy environments through use of lip reading (Crane & Ferrari, 2015; Drijvers & Özyürek, 2017; McGettigan et al., 2012). During decision making, cross-modal stimulation can prime attention in receivers to improve performance (James et al., 2022).

Additional information, however, will enhance performance only if the brain is able to associate the various stimuli it is receiving, correctly assign them to their particular source and make informed decisions based on the totality of information in the stimuli. Nonredundant or ambiguous multimodal cues may hinder, rather than help, decision making if they overwhelm cognitive processing or obscure signal—source associations (Smith et al., 2023). Cue integration can also lead to novel, overriding, or even conflicting responses depending on cue reliability and redundancy (Smith et al., 2023). If there is too much information to analyse, the individual may experience a phenomenon known variously in human psychology as information, cognitive or perceptual overload (Talsma et al., 2010). This overload may result in decreased performance or even maladaptive decisions by the receiver. We refer to this general phenomenon as the cognitive overload hypothesis.

Despite said theoretical predictions, we have little understanding under which circumstances attending to multicomponent cues enhances decision-making performance or reduces it by creating cognitive overload. We addressed this question with a behavioural experiment wherein predators made foraging decisions while attending to ambiguous information with and without additional components. Specifically, we were interested in how additional streams of information may be used when the primary stream combines both positively and negatively associated stimuli. Such cases of cue ambiguity are particularly ecologically relevant and remain understudied in sensory ecology (Smith et al., 2023).

The predatory fringe-lipped bat, *Trachops cirrhosus*, foraging on frogs is an ideal system to ask how predators use multicomponent prey-derived and social cues to make foraging decisions in noisy environments (Page et al., 2014; Surlykke et al., 2013). This Neotropical bat commonly hunts by passively eavesdropping on auditory prey cues (Tuttle & Ryan, 1981), but it flexibly adopts echolocation-derived information from the target when challenged in the laboratory (Gomes et al., 2016; Halfwerk, Dixon, et al., 2014; Halfwerk, Jones, et al., 2014) and rapidly adopts new hunting behaviour through social learning (Jones et al., 2013; Page & Ryan, 2006; Patriquin et al., 2018). When hunting frogs, it uses information in a frog's call to choose palatable versus poisonous frog species (Page et al., 2012; Page & Ryan, 2005; Tuttle & Ryan, 1981). For example, the leaf-litter toad, *Rhinella alata* (formerly *Bufo typhonius*), and the túngara frog, *Engystomops pustulosus* (formerly *Physalaemus pustulosus*), overlap in range and size, but *R. alata* secretes a potentially lethal poison (Rodriguez et al., 2021). *Trachops cirrhosus* bats have shown a strong preference for túngara frogs and a strong distaste for *R. alata* when accidently consumed (Page et al., 2012; Tuttle & Ryan, 1981).

Túngara frog displays provide one of the best studied systems of sexual selection and predation (Ryan, 1985, 2011, pp. 185—203; Ryan et al., 2019). Male túngara frogs court females with a multimodal display: their calls (auditory) and the simultaneously inflating vocal sac (visual) create water ripples (seismic) (Halfwerk, Jones, et al., 2014). The combined visual and seismic cue is behaviourally relevant for females choosing between two courtship calls in a phonotaxis assay (James et al., 2022) as well as by hunting *T. cirrhosus* (Gomes et al., 2016; Halfwerk, Jones, et al., 2014; Rhebergen et al., 2015). In contrast to the female frogs, the bats perceive the additional display components with echolocation (Gomes et al., 2016; Halfwerk, Jones, et al., 2014; Rhebergen et al., 2015). Even though frog calls and echoes are both acoustic signals, they are perceived through functionally different modalities, since auditory input from ‘passive’ listening (to an external sound source) and from ‘active’ listening (to echoes of self-generated sound) present two segregate streams of information (Barber et al., 2003) that are processed differently in the auditory system (Goerlitz et al., 2008; López-Jury et al., 2021). Overall, echolocation-derived information offers bats a distinct information stream about potential targets compared to passive listening. This ecological example illustrates how different sensory channels, even within the same physical domain, can constitute nonredundant, and potentially conflicting, inputs (Smith et al., 2023).

In the present study, we evaluated decision making of six fringe-lipped bats attending to ambiguous information with additional cues. Across a series of six treatments, we quantified bats’ foraging decisions in response to synthesized hybrid calls spanning a gradient from the call of the palatable túngara frog to that of the poisonous toad *R. alata*. For the six treatments, three types of stimuli and combinations thereof were added: a social cue (conspecific chewing noises), environmental noise (anuran chorus) and a prey-derived target cue for echolocation (vocal sac motion and water ripples). We predicted that (1) the social and target cues would make a hybrid call more attractive as a potential food source and that (2) decisions would be slower in the presence of noise. By simulating a naturalistic sensory conflict and layering social, environmental and prey-derived cues, our study provides an experimental test of real-world multicue decision making, an area recently emphasized as a frontier in behavioural and cognitive ecology (Smith et al., 2023).

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METHODS

Ethical Note

We trained and tested six adult, male *T. cirrhosus*, caught between January and May 2023 from Soberanía National Park, near Gamboa, Panamá, in either mist nets or in their day roosts. Bats were kept individually at the Smithsonian Tropical Research Institute, in a large open-air flight cage (5 × 5 × 2.5 m) with one corner closed off by dark cloth to provide a sheltered roost and perch (Fig. 1a). Water was always provided ad libitum from an artificial pool. Bats were fed a minimum of 10 g of fish per night during experimental sessions. Upon release into the flight cage, bats were allowed to acclimate to captivity, trained to respond to auditory stimuli (see Experimental Design below) and tested for 4–6 nights of data collection. Four of the six bats had participated in previous, unrelated experiments; these animals were included to reduce overall capture numbers in line with the 3Rs (Reduction), as prior training did not influence behaviour in the current paradigm. Experimental trials were conducted during the bats' active nocturnal period. Handling was kept to a minimum, and bats were never restrained or subjected to invasive procedures during the study. At the end of the experiment, no longer than 14 days after capture, bats were injected subcutaneously on the back with a passive integrated transponder tag (APT12 PIT tag, 12.5 mm, ~0.1 g and ~0.3% of body mass; Biomark, Boise, ID, U.S.A.) to prevent retesting and returned to the wild at site of capture in apparent good health. All experiments and husbandry adhered to the ASAB/ABS Guidelines for the Use of Animals in Research (ASAB Ethical Committee/ABS Animal Care Committee, 2024), followed the legal requirements of Panamá, and were licensed and approved by the Institutional Animal Care and Use Committee of the Smithsonian Tropical Research Institute (IACUC numbers SI-21012 and SI-23001) and the Government of Panamá (Ministerio de Ambiente permit ARG-078-2022). Our study was designed to minimize potential stress, following principles of Refinement and animal welfare best practices. The use of wild-caught bats was necessary due to the ecological and behavioural specificity of the research question, and no alternatives to live animal testing were appropriate. The total number of individuals was kept to a minimum required for robust inference.

Experimental Set-up

This work was conducted with the support of the Smithsonian Tropical Research Institute (STRI) in Gamboa, Panamá, a field station that provided housing, logistical support and experimental facilities. We used an automated robofrog system (for details, see James et al., 2022; Taylor et al., 2008) to mimic the components of the túngara frog courtship display: calls, vocal sac movement and water ripples. A three-dimensional frog model was placed at the rim of an artificial pool consisting of a rectangular tray (50 × 70 cm), raised 15 cm above the ground and filled with water (~1.5 cm deep). A loudspeaker (Fostex FE103En 4-inch, Foster Electric Company, Tokyo, Japan) was placed directly beneath the frog model under the pool ('robofrog speaker'). An inflatable silicone vocal sac replica was mounted to the frog model's front and attached to a compressed air system to inflate and deflate. A custom-built ripple generator was placed inside the pool in front of the model, below the water surface. The playback of the frog call (acoustic stimulus), inflation of vocal sac and generation of water ripples (echo-acoustic stimuli) were synchronized, thereby mimicking the courtship display of a live male. The model and pool were placed in the centre of the flight cage, approximately 3.5 m from the roost, which served as the bat's starting point for each trial (Fig. 1a). In addition to the robofrog speaker, five more loudspeakers provided the background audio for respective treatments. One speaker was mounted on the ceiling 2.5 m above the robofrog to mimic a perched conspecific bat chewing food ('bat speaker'). Four speakers were placed on the floor along the four walls approximately 3 m from the robofrog to mimic a large mixed-species anuran chorus ('chorus speakers').

Visual surveillance and technical equipment were operated from a room adjacent to the flight cage. Trials were monitored under infrared illumination (CM-IR-130-850NM, CMVision Technologies Inc, Houston, TX, U.S.A.): one camera (HDR-CX560, Sony Group Corporation, Tokyo, Japan) provided a close-up view of the bat in the shelter area to ensure the bat's alertness at the beginning of each trial, and another camera (FDR-AX53, Sony Group

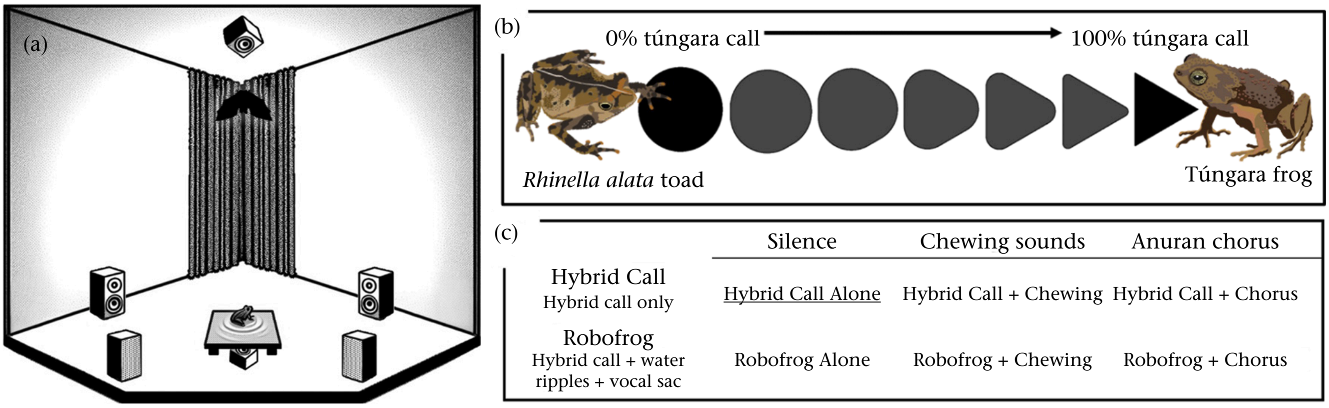

Figure 1. The experimental design using a Go/No-go paradigm to evaluate bats' decision in response to hybrid calls broadcast by a robofrog under six different treatments. (a) Bats attacked from a perch 2.5 m above and in front of a robofrog baited with pieces of fish, inside a small pool of water. Hybrid calls were played from a speaker below the robofrog, and background audio was played from speakers on the floor (anuran chorus) or the ceiling (conspecific chewing). Diagram not to scale. (b) The anuran calls used as acoustic stimuli varied in their composition. The call of the edible túngara frog (black triangle) served as positive control; the call of the poisonous leaf-litter toad *R. alata* (black circle) served as negative control. A series of hybrid túngara/toad calls (grey symbols) ranging from 5 to 100% túngara were spontaneously evaluated by the bats for their representation of suitable prey in a Go/No-go paradigm. Anuran illustrations by Damond Kyllo. (c) Treatments consisted of hybrid call conditions wherein only an acoustic stimulus was broadcast, and robofrog conditions wherein the robofrog broadcast the acoustic stimulus simultaneously with movement of its synthetic vocal sac and ripples on the water surface. The three background noise conditions were silence (no added background sounds), conspecific chewing sounds and a mixed-species anuran chorus. The Hybrid Call Alone treatment (underlined) served as the baseline.

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Corporation) provided a view of the entire flight cage, recording each bat's responses to the presented stimuli.

Experimental Design

Bats were presented with three types of calls (Fig. 1b): the call of the edible túngara frog (hereafter 'túngara'; positive control), the call of the similarly sized but poisonous leaf-litter toad (hereafter 'toad'; negative control) and a series of synthesized calls intermediate between the two species for spontaneous evaluation (test trials, hereafter 'hybrid'). Taking advantage of the natural preference of *T. cirrhosus* for the túngara frog call (Tuttle & Ryan, 1981), we used a Go/No-go paradigm to examine each bat's decisions to attack the frog model. In a Go/No-go task, animals are either presented with a stimulus associated with a reward (the 'Go' stimulus, here the 100% túngara call) or another stimulus that triggers response inhibition (the 'No-go' stimulus, here the 100% toad call). By presenting bats with hybrid calls that lie along a continuum between Go and No-go stimuli and recording their response, we evaluated their perception of these ambiguous stimuli. We broadcast each hybrid call under six different experimental treatments (Fig. 1c): (1) Hybrid Call Alone (hybrid call only, serving as baseline), (2) Hybrid Call + Chewing Sounds, (3) Hybrid Call + Chorus, (4) Robofrog Alone (hybrid call, vocal sac movement and presence of water ripples), (5) Robofrog + Chewing Sounds and (6) Robofrog + Chorus. For robofrog treatments, the onset of the call from the robofrog speaker was synchronized with the simultaneous vocal sac and ripple cues, independent of hybrid call composition.

For each bat, the natural preference to attack the robofrog when a túngara call is broadcast was confirmed and/or reinforced with a food reward (a piece of fish placed on the back of the frog model) until an attack rate of 100% was achieved. Similarly, the natural aversion to the call of the unpalatable toad was confirmed and/or reinforced with punishment (a piece of fish coated with ascorbic acid powder; Video S1) until a No-go rate of 100% was achieved. After these positive and negative control stimuli were established, bats were tested for their spontaneous decision to attack the frog model when it was broadcasting a random hybrid call (experimental workflow outlined in Supplementary Fig. S1). These hybrid trials were unrewarded. Every three to four hybrid trials were followed by one control trial, where either the punished negative control stimulus or the rewarded positive control stimulus was broadcast. This way, bats were fed during the experiment and their motivation to fly to a positive stimulus was assessed. The control trials also served as data validation checkpoints throughout the experimental session. Each session ended when the bat was no longer motivated to feed. Most bats were able to complete three sessions of data collection per night with time in between to digest.

To mimic a natural foraging situation, each trial began with exposing the bat to either the anuran chorus (+Chorus treatments) or silence (all other treatments). After a period of 2–3 s, the presentation of hybrid calls and respective additional signals (vocal sac, ripples and/or conspecific chewing sounds) was switched on (in addition to the background chorus treatment for +Chorus treatments). The trial ended either when the bat left its perch inside the roost and attacked the frog model (Go; Video S2) or when the playback stopped after 15 s without the bat leaving its perch (No-go). We recorded the bat's choice as well as its latency to flight (time (s) between the initiation of hybrid stimuli and the bat leaving its perch). In rare cases in which it was unclear whether the flying bat had attacked the frog model or not, the trial was voided and repeated later. Following a Go trial, the bat flew back to its perch and (in the case of a rewarded positive control trial) was allowed to eat and briefly groom before the next trial was started. If a bat failed a control trial (i.e. flew to a negative control or did not fly to a positive control), all previous hybrid trials since the last control trial were excluded from analysis. We conducted trials in this way for multiple subsequent nights until bats no longer voluntarily participated in the experiment due to satiation (Supplementary Fig. S1).

Acoustic Signals

The experiment used acoustic signals as stimuli and as treatments. All acoustic signals were generated offline and stored in a data structure. During the experiment, randomly chosen versions/segments of each respective acoustic signal were loaded into the sound presentation program with a custom MatLab R2021a application (The MathWorks, Inc., Natick, MA, U.S.A.) running a SoundMexPro plugin (HörTech GmbH, Oldenburg, Germany) on a single laptop (ThinkPad L450, Lenovo). Signals were then sent through a multichannel audio interface (Behringer U-Phoria UMC1820, Music Tribe, Manila, Philippines) and three stereo amplifiers (N22 AudioEngine) to the respective loudspeakers (robofrog speaker, bat speaker, chorus speakers; Fig. 1a). Audio outputs were calibrated with a hand-held SPL meter (33–2055, RadioShack; set to C-weighted, fast, maximum) at the start of each night.

The túngara-only stimulus used as a positive control was one call randomly picked from a set of 10 recordings of a standard túngara call ~400 ms in length. The toad-only stimulus used as a negative control was one call randomly picked from a set of five recordings of a standard *R. alata* call ~400 ms in length as well. This approach aimed to introduce some natural variation in call variants while maintaining consistency in call structure and duration. The hybrid calls used in experimental trials were created from these 10 túngara calls and five toad calls. One túngara call was digitally blended together with one toad call by relative amplitude, and this process was repeated in 5% intervals from 5% to 95% túngara for all 50 túngara–toad call combinations. For instance, túngara call at 95% total sound level was mixed with toad call at 5% total sound level, then túngara call at 90% total sound level mixed with toad call at 10% total sound level, etc. This procedure yielded 19 versions of 50 hybrid calls each, resulting in 950 hybrid call mixes in total. Note, however, that a bat was not necessarily presented with the full set of mixes. All call files (controls and hybrids) were digitally resampled to a sampling rate of 20 kHz, RMS-normalized and broadcast from the robofrog speaker. Playback level of the hybrid calls was 76 dB SPL RMS re. 20 µPa at 1 m (Halfwerk, Dixon, et al., 2014).

The signal used for the +Chewing treatment was a 15 s segment cut out of one of 10 recordings of a *T. cirrhosus* bat chewing on food. These recordings had been resampled to 44.1 kHz, filtered (7 kHz high-pass, 6 dB roll-off; Audacity 3.4.2, audacityteam.org) and edited to achieve permanent monotonous chewing sounds without any sudden events or resemblance to the anuran chorus. All segments were RMS-normalized and broadcast from the ceiling speaker. Playback level of the conspecific chewing sounds was 68–72 dB SPL RMS re. 20 µPa at 1 m.

The four signals used for the +Chorus treatments were four 15 s segments each randomly cut out of a different recording randomly chosen out of 10 recordings of a mixed-species anuran chorus (consisting of calls from the palatable túngara and *Dendropsophus ebraccatus* frogs, and the unpalatable R. alata toad). These recordings had been resampled to 44.1 kHz. All segments were RMS-normalized. Each of the four segments was broadcast from one of the four chorus speakers. Playback level of the chorus sounds was the same as the hybrid calls (76 dB SPL RMS re. 20 µPa at 1 m).

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Data Analysis

All analyses were performed using R Statistical Software (version 4.2.2; R Core Team, 2024). All models were mixed effects regressions run using the ‘lme4’ package (version 1.1−31; Bates et al., 2015). All analyses excluded voided trials as well as positive and negative control trials.

To examine the effects of both acoustic stimuli and treatments on bats' overall attack probability, we ran a generalized linear mixed effects regression (GLMER) model with a binomial distribution and using the BOBYQA optimizer (Powell, 2009). The response variable in this model was the bat's choice within a given trial (Go or No-go). The model's fixed effects were (1) the composition of the acoustic stimulus (i.e. % túngara call within the hybrid stimulus), (2) the treatment and (3) the interaction of stimulus composition and treatment. The identity of each bat was included as a random effect. The model was analysed with a type II Wald chi-square test. We also ran generalized linear models (GLM; with a binomial error family) on the data from each bat individually. We ran a similar model on a subset of the data with the greatest stimulus ambiguity (40−60% frog versus toad), with treatment as the sole fixed effect.

We also analysed whether treatment had an effect on bats' attack thresholds. We define two types of attack thresholds: first, the ‘decision threshold’ is the percentage of túngara call in the hybrid stimulus at the 50% attack mark along a bat's fitted decision curve (see Results, dashed line in Fig. 2a). Second, the ‘minimum approach threshold’ is the lowest percentage of túngara call in the hybrid stimulus at which a bat would still attack that stimulus at all, i.e. display an attack rate greater than 0%. To examine whether different treatments influenced bats' attack thresholds, we ran two linear mixed effects regression (LMER) models. The response variable in these models was the ‘decision threshold’ or the ‘minimum approach threshold,’ respectively, in the percentage of túngara call. Both models' sole fixed effect was the treatment of the trial, and the identity of each bat was included as a random effect. Individual treatment results were compared against the Hybrid Call baseline treatment using *t* tests (Satterthwaite's method).

To examine the effects of both acoustic stimuli and treatments on bats' latency to flight, we ran another GLM model on validated Go trials in which bats had attacked an acoustic signal. Latency was measured in seconds from the onset of hybrid acoustic signals to the moment a bat left the perch to initiate an attack and was our response variable in all models. The model's fixed effects were (1) the composition of the acoustic stimulus (i.e. % túngara call within the hybrid stimulus), (2) the treatment and (3) the interaction of stimulus composition and treatment. The identity of each bat was included as a random effect, and we used a gamma error family with a log link function given the distribution of the data. Results were analysed with type II chi-square tests. We also ran generalized linear models on the data from each bat to assess interindividual variation in behaviour and conducted post hoc contrasts using Tukey's tests. Six validated hybrid trials were omitted from latency analyses due to flight timing recording errors. We also ran a similar model on a subset of the data with the greatest stimulus ambiguity (40−60% frog versus toad), with treatment as the sole fixed effect.

To determine whether bats learned over time or had become accustomed to certain stimulus/treatment combinations, we included the amount of exposure a bat had to a given combination in earlier iterations of our models. We found no evidence of exposure influencing latency to flight or decision data in any way, and as such excluded it from our final analyses.

RESULTS

Six male *T. cirrhosus* bats completed 1705 valid trials in the Go/No-go experimental paradigm, in which they decided whether or not to attack a frog model broadcasting hybrid calls containing varying degrees of edible frog call and poisonous toad call. Each individual performed 22−66 (median 49) valid hybrid trials per treatment, and thus 155−353 (median 295) valid hybrid trials across all six treatments (Supplementary Fig. S2).

We used the behavioural response of the foraging bats to assess the effects of our treatments on their baseline decision making. The six treatments consisted of the following stimulus

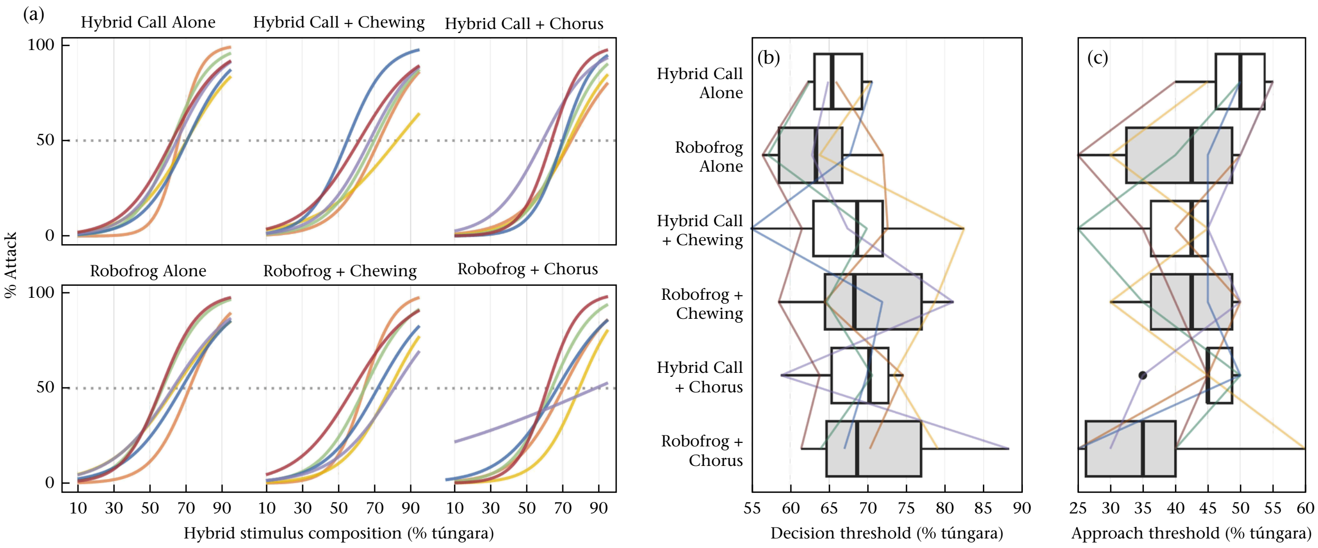

Figure 2. Bats' foraging decisions across all treatments. Each coloured line represents an individual bat. (a) Bats' attack frequencies towards the frog model when the model broadcast a hybrid call composed of a varying percentage of túngara call across the six treatments. Curves are fitted to the binary responses of bats for each of the hybrid stimuli. Dotted horizontal line intersects bats' decision curves at the decision threshold. (b) Percentage of túngara call in the hybrid stimulus at which a bat was likely to attack 50% of the time (decision threshold). (c) Percentage of túngara call in the hybrid stimulus required to elicit at least one attack (minimum approach threshold) for each treatment. Boxes in (b) and (c) depict interquartile ranges of thresholds within each treatment, and black bars in boxes represent median values. Note that decision thresholds were derived from fitted decision curves, but approach thresholds were derived from the raw Go decisions.

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combinations: (1) Hybrid Call Alone (serving as baseline), (2) Hybrid Call + Chewing Sounds, (3) Hybrid Call + Chorus, (4) Robofrog Alone (hybrid call, motion of vocal sac and water ripples), (5) Robofrog + Chewing Sounds and (6) Robofrog + Chorus. We evaluated bats' attack behaviours across treatments based on two types of attack thresholds: the 'decision threshold', the hybrid stimulus at which a bat would attack 50% of the time as calculated from that bat's fitted attack curve; and the 'minimum approach threshold', the minimum % túngara hybrid call at which bats decided to attack a signal.

Validation of Control Stimuli

To ensure consistency in stimulus presentation while allowing for natural acoustic variation, we used multiple variants for both the rewarded and aversive control stimuli. The positive control (100% túngara) was randomly drawn on each trial from a set of 10 standardized túngara call recordings (~400 ms), while the negative control (100% *R. alata*) was drawn from a set of five standardized *R. alata* calls (~400 ms). Across all six bats, we recorded 87 instances in which individuals failed to respond to the túngara control (i.e. did not approach), and just three instances in which a bat failed to avoid the *R. alata* control. All three errors in the negative control occurred in the same individual, and each involved a different *R. alata* variant. To assess whether certain variants may have been more or less effective, we conducted a chi-square test across the 10 túngara variants. This revealed no significant difference in failure rates ($\chi^2_9 = 15.45$, $P = 0.079$), indicating that the bats did not preferentially respond to specific versions of the control stimuli. The occasional imbalance in trial numbers for the +Chewing and +Chorus treatments was due to rare, random interruptions (e.g. equipment or environmental interference), and we verified that these instances did not systematically affect response patterns. Taken together, these results support the reliability and balance of our control stimuli across treatments.

Attack Probability

We first asked how the probability that a bat decided to attack the frog model was influenced by the composition of the broadcast hybrid stimulus, i.e. relative amplitude of the edible túngara frog call compared to the poisonous leaf-litter toad call. Confirming our expectations, we observed a strong main effect of acoustic stimulus composition, with bats more likely to attack hybrid stimuli containing a higher percentage of túngara call (ANOVA: $\chi^2_1 = 406.1$, $P < 0.001$; Fig. 2a, Supplementary Table S1), but we found no significant effect of treatment ($\chi^2_5 = 7.2$, $P = 0.21$) and no interaction between stimulus composition and treatment ($\chi^2_5 = 3.7$, $P = 0.60$). When we restricted our analyses to the most ambiguous stimuli (40–60% frog), we continued to find no effect of treatment ($\chi^2_5 = 7.4$, $P = 0.19$; Supplementary Table S2). Because of the large number of trials we ran on each bat, we were also able to conduct models on each bat individually. The statistical conclusion was identical across each bat: there was a significant effect of stimulus composition ($\chi^2_1 > 38.0$, $P < 0.001$ for all), but no significant effect of treatment ($\chi^2_5 < 9.0$, $P > 0.14$) and no interaction ($\chi^2_5 < 7.0$, $P > 0.28$; Supplementary Table S3).

Decision and Minimum Approach Thresholds

We next asked how the treatment influenced a bat's decision threshold, i.e. the minimum percentage of túngara call in a hybrid stimulus at which an individual bat would attack 50% of the time. We found no evidence of differences that decision threshold values in any treatment differed from the baseline Hybrid Call Alone treatment (range 63.3–70.2% túngara call, $P > 0.15$ for all; Fig. 2b, Supplementary Table S4). However, bats displayed the least variation in decision thresholds between individuals under the Hybrid Call Alone baseline treatment.

We next asked how the treatment influenced a bat's minimum approach threshold. Under the Hybrid Call Alone baseline treatment, bats never attacked signals containing any less than 40% túngara call. However, their minimum attack thresholds were lower under the Robofrog + Chorus treatment, attacking hybrid calls that were 12.5% more toad-like (SE = 5.2; $t_{30} = -2.42$, $P = 0.022$; Fig. 2c, Supplementary Table S5). We also observed that bats had slightly lower minimum approach thresholds under the Hybrid Call + Chewing (attacking hybrid calls that were 10% more toad-like; SE = 5.2; t test: $t_{30} = -1.93$, $P = 0.063$) and Robofrog Alone treatments (attacking hybrid calls that were 9.2% more toad-like; SE = 5.2; t test: $t_{30} = -1.77$, $P = 0.087$), although these effects were not as strong.

Latency to Flight

For trials that resulted in an attack, we further asked whether the bats' latency to leave the roost and initiate the attack was affected by hybrid call composition or treatment. We found that bats flew more quickly to attack hybrid stimuli with a higher percentage of túngara call (ANOVA: $\chi^2_1 = 72.8$, $P < 0.001$; Fig. 3, Supplementary Table S6). We further found that treatment had no overall effect on latency to flight ($\chi^2_5 = 5.6$, $P = 0.34$) and there was no interaction between treatment and hybrid stimulus composition ($\chi^2_5 = 5.1$, $P = 0.40$). When restricted our analysis to the most ambiguous stimuli (40–60% toad), we continued to find no significant effect of treatment ($\chi^2_5 = 3.6$, $P = 0.61$; Supplementary Table S7). Because of our deep sampling of behaviour within each bat, we were also able to conduct models limited to each individual, and we continued to find a significant effect of call composition on the latency to leave the roost for five of the six bats ($\chi^2_1 = 4.3$, $P < 0.038$ for all) and a marginally nonsignificant effect for the final bat ($\chi^2_5 = 3.2$, $P = 0.073$; Supplementary Table S8). Interestingly, we also observed a significant effect of treatment for one bat ($\chi^2_5 = 14.5$, $P = 0.013$), with post hoc contrasts indicating faster latencies in both chewing treatments compared to the Hybrid Call Alone treatment (Tukey's tests: $P < 0.035$ for both).

DISCUSSION

The fitness consequences of animal decisions, from foraging to mating to finding shelter and avoiding predators, are far-reaching. Fringe-lipped bats use information in prey calls to distinguish between palatable versus poisonous prey items (Page et al., 2014; Tuttle & Ryan, 1981). In the current study, we presented *T. cirrhosus* with a series of hybrid stimuli and found that they attacked stimuli with greater percentages of edible túngara call more frequently and more quickly. Between our experimental reinforcement training and any previous aversion that bats may have learned in the wild, hybrid stimuli containing less túngara call and more toad call were less attractive. These behavioural responses to the auditory stimulus were reliably observed across different treatments that included additional sensory cues: conspecific acoustic cues, anuran chorus acoustic stimuli and prey movement cues from an artificial vocal sac inflation and water ripples. In the following sections, we first discuss the influence of our experimental treatments on both attack decisions and latencies. We then consider our results in the context of the cognitive overload hypothesis, and finally address the benefits of the Go/No-go paradigm with negative reinforcement.

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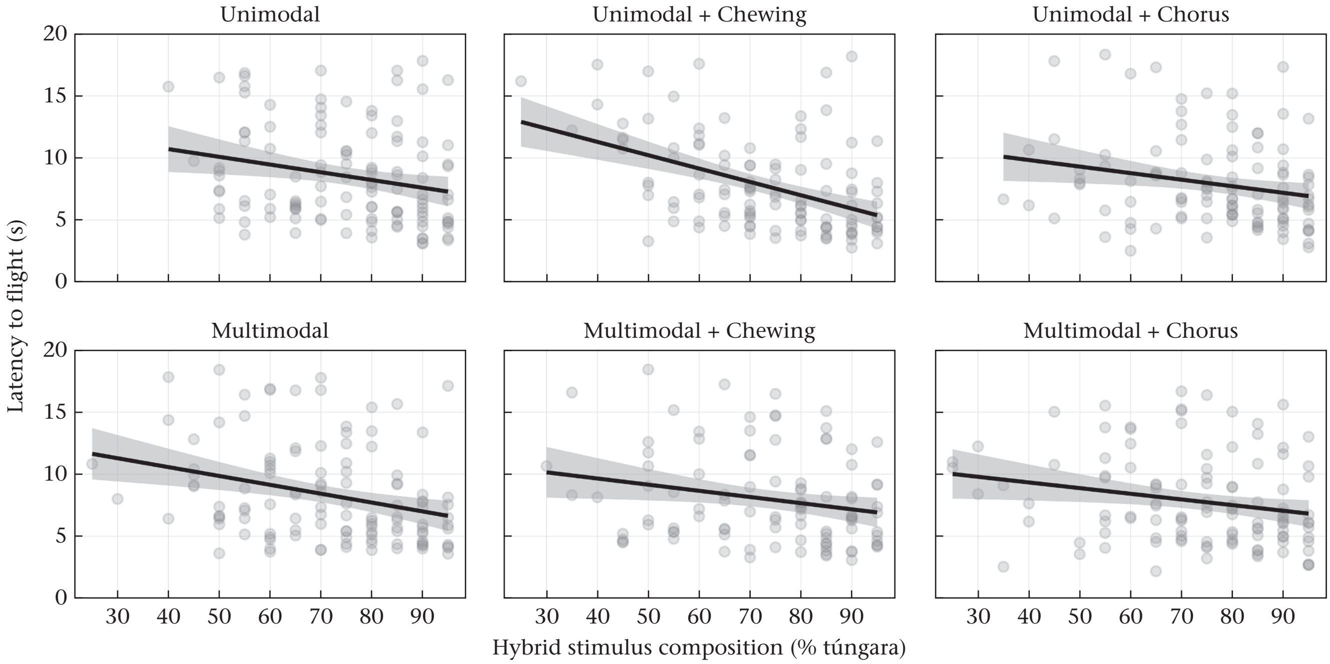

Figure 3. Bats' latency to flight in response to hybrid stimuli with varying percentages of túngara call across treatments. Shaded regions represent 95% CI. Latency data were only available for hybrid trials in which bats attacked during Go responses; all No-go responses were therefore excluded here.

Consistent Decision Making across Treatments Incorporates Behavioural Flexibility

Contrary to our prediction that the addition of information would influence bats' decision making, all bats displayed decision thresholds at similar points along the túngara–toad gradient across all treatments (Fig. 2b). We had anticipated that the addition of social cues (conspecific chewing sounds) would make the bats more likely to attack lower-percentage túngara stimuli. Hearing a conspecific eating may heighten general motivation levels to forage, or signal to the focal bat that palatable prey is nearby, thereby positively influencing the perception of the hybrid stimulus as more like a túngara call. Likewise, we had expected that the addition of target cues for echolocation (vocal sac movement and water ripples) would shift bats' decision thresholds towards lower-percentage túngara stimuli for numerous reasons: First, the quality of both the vocal sac and the ripple movement was based on an actual calling túngara frog (*R. alata* toads do not call from water and thus do not produce ripples) and remained constant for all hybrid calls, potentially cueing the bats to the presence of a palatable frog. Furthermore, the added target cues should have made the túngara component of the hybrid stimulus more attractive and easier to localize for the bats (Halfwerk, Dixon, et al., 2014; Halfwerk, Jones, et al., 2014; Rhebergen et al., 2015). Overall, the robustness of decisions against influences from additional cues is consistent with a previous study demonstrating rational decisions even when confronted with complex choice scenarios (Hemingway et al., 2017).

In contrast to the decision thresholds, however, the minimum approach thresholds of some bats did shift. The range of stimuli that the bats were willing to attack at all was narrowest under the Hybrid Call Alone treatment (Fig. 2c), where bats never attacked a hybrid stimulus that contained less than 40% túngara. In contrast, with the addition of anuran chorus noise and robofrog target cues (Robofrog + Chorus treatment), some bats flew on signals containing as little as 25% túngara (Fig. 2c). While we intended the anuran chorus noise to challenge the bats' attention to the target speaker, it is possible that this also suggested an increased likelihood of finding a prey.

Individual differences in approach behaviour when additional cues were present may stem from variations in how individuals manage uncertainty (Bartumeus et al., 2016; Crane et al., 2024). As Mathot et al. (2012) outlined, animals facing uncertain or ambiguous stimuli can adopt diverse strategies, including increased sampling effort, insurance-based caution or variance sensitivity. In our study, some bats appeared to adopt a more exploratory approach by attacking stimuli with lower túngara content in the presence of additional cues, a behaviour consistent with either a sampling or variance-sensitive strategy. Conversely, other individuals maintained a more conservative attack threshold, potentially indicating risk-averse tendencies or a greater reliance on insurance tactics. To evaluate whether additional cues had a stronger influence under ambiguity, we conducted a focused analysis limited to trials with hybrid calls containing 40–60% túngara content. However, this analysis did not reveal a significant effect of treatment. While this suggests that additional cues did not uniformly influence decision making under ambiguous conditions, the persistent individual variation in response strategies remains notable. This behavioural variation in response to added complexity is particularly intriguing given that all bats experienced identical training and experimental conditions in the laboratory. However, since all individuals were wild caught, they likely differed in prior experience with prey types and acoustic cues. Therefore, we interpret this variation not as random noise but as potentially adaptive differences in behavioural plasticity linked to how individuals weigh uncertainty and risk.

Latencies to Flight Reflect Stimulus Composition Consistently across Treatments

The strong positive effect of hybrid stimulus composition on attack latencies reflects the bats' preference for túngara as a prey item compared to the toad, as *T. cirrhosus* have demonstrated significantly shorter attack latencies for more preferred stimuli in previous studies (Fugère et al., 2015; Hemingway et al., 2019). Beyond this baseline preference for palatable prey, the observed latencies in our study reflect the phenomenon known as a speed−accuracy trade-off: bats increased their latencies for hybrid calls containing less túngara and more toad. Typically, slow decision making is thought to aid accuracy at the risk of missing opportunities and prolonged exposure to predators, while fast decision making might be less accurate and thereby riskier in itself (Chittka et al., 2009). Facing the penalty of foul-tasting bait, the bats thus sacrificed speed when the stimulus became more ambiguous (Fig. 3).

In line with this notion, we had expected treatment to similarly impact latency to flight, with bats flying more quickly under treatments with added social or target cues but taking more time to make a decision in treatments with added acoustic complexity. Counter to those expectations, flight latencies were consistent across treatments (Fig. 3), although we note that one bat had significantly faster latencies in both +Chewing treatments compared to the Hybrid Call Alone treatment. While a difference in latencies between Hybrid Call Alone and +Robofrog treatments in general was not expected (Gomes et al., 2017; experiment 1 in Rhebergen et al., 2015), we were surprised to find no effect of the +Chorus treatments. Two earlier robofrog studies demonstrated that under noise, *T. cirrhosus* attacks with shorter latencies when the vocal sac cues are available (a frog chorus in experiment 2 in Rhebergen et al., 2015; túngara masking noise in Gomes et al., 2016). Without the vocal sac cues, however, these studies reported that latencies in noise were longer than in silence (Gomes et al., 2016; experiment 2 in Rhebergen et al., 2015). Contrary to those results, we did not see longer latencies in the acoustic complexity treatment in the present study, nor were longer latencies found in a study of *T. cirrhosus* foraging in white noise (Page & Ryan, 2008).

Decision Making in the Framework of the Cognitive Overload Hypothesis

Many animals interact with their environment through more than one sensory channel. Fringe-lipped bats often forage in complex environments and can integrate and weigh different cues across different information streams (Gomes et al., 2016; Halfwerk, Dixon, et al., 2014; Halfwerk, Jones, et al., 2014). We still have little understanding of how information in one stream influences decisions that an animal makes with information from another information stream. Theoretically, attending to multiple sensory cues while making decisions could either enhance an animal's performance or hamper it by creating a cognitive overload. In the current experiment, the addition of multicomponent target prey cues, for instance, could lead the bats to either make better decisions because of an enhanced discrimination ability or make worse decisions because of an overwhelmed cognitive system. This effect itself might be influenced by the presence of further sensory information in the form of conspecific cues or background noise. However, our results showed that neither attack decisions nor latencies differed across treatments that added additional cues.

The most straightforward explanation for these findings would be active stimulus filtering. Animals have mechanisms to decrease the amount of information that is processed to avoid cognitive overload (von der Emde & Warrant, 2016; Warrant, 2016). As actively sensing animals, echolocating bats are especially adept at extracting relevant sensory information in noisy environments (Corcoran & Moss, 2017; Page & ter Hofstede, 2021). It seems possible the bats received enough relevant information about the identity of the unknown prey item from hybrid calls alone to make their decisions and they could effectively ignore any additional information presented to them. However, among all treatments, bats displayed the least individual variation in decision thresholds under the Hybrid Call Alone control treatment and demonstrated more flexible behaviour when the information landscape became more complex.

Assuming then that bats did take additional information into account, how would decision making impaired by cognitive overload present itself? A ‘worse’ decision could be an attack on a stimulus containing more toad call, signifying more dangerous prey. However, a ‘worse’ decision could also be not attacking an ambiguous stimulus, because it could mean missing out on a meal. The evaluation of a particular decision's quality might differ between individuals and even within individuals depending on individuals' current hunger state, and thus may have been undetected in our current experiment.

Attacking a distasteful or poisonous prey item is not necessarily a fatal mistake. Although toad venom may be lethal to the bats if ingested (Chen & Kovaříková, 1967; Rodriguez et al., 2021), *T. cirrhosus* that attacked prey covered in *R. alata* venom rejected the prey after contact, but prior to consumption, and suffered no apparent adverse effects from the encounter besides increased saliva production (Page et al., 2012). Bats did not appear to sense the noxious chemical cues prior to attack, as the distasteful prey was only rejected postcapture (Page et al., 2012). Similarly, during our negative control reinforcement trials, we did not observe *T. cirrhosus* reacting to ascorbic acid powder prior to physical contact (ascorbic acid, like the toxins found in *R. alata*, is a nonvolatile compound). Any bat that did attack 100% toad calls, whether due to naïvety or hunger, immediately rejected the bait item and showed apparent distaste by lip smacking and body shuddering (Video S1). These responses suggest that although *T. cirrhosus* may not consume poisonous prey items, the cost for attacking them is relatively low. Their ability to sense and reject poisonous prey postcapture without suffering major consequences likely accounts for this bat's high levels of behavioural flexibility in foraging (e.g. Page & Ryan, 2005), and for the frequency at which *T. cirrhosus* attacked signals containing relatively low percentages of túngara calls in the present study. As such, neither the benefits of enhanced discrimination on the one hand, nor the need for conservative decision making to avoid costly mistakes on the other hand, appear to be heavily weighted factors in this bat's foraging behaviour.

Go/No-go Paradigm with Negative Reinforcement

Prior studies examining *T. cirrhosus* foraging decisions and preferences used two-alternative forced-choice experiments (e.g. Fugère et al., 2015; Jones et al., 2013; Ryan et al., 1982), which give rise to issues of side bias limiting the number of valid trials obtained from a given individual, requiring countertraining to break the bias before being able to proceed with the experiment (see methodology section in Hemingway et al., 2018). Our experimental design avoided the obstacle of side bias by introducing a Go/No-go paradigm wherein the binary decision of whether or not to attack was then used to answer preference questions. This set-up allowed us to conduct many more trials than would have been possible otherwise and resulted in a large number of trials for each individual bat. We recommend future studies to consider our experimental design to circumvent side biases and conduct a more efficient experimental process in general.

Conclusions

In summary, our work offers valuable insights into decision making in noisy environments. We have introduced a Go/No-go paradigm to assess the foraging decisions of a predatory bat in response to ambiguous prey cues in the presence of additional stimuli. We demonstrated that both attack decisions and latencies to attack were highly consistent across bats and across treatments, supporting neither the enhanced performance nor the cognitive overload hypotheses on decision making. We saw flexibility in minimum approach thresholds, however. Bats showed exploratory and risk-taking behaviour (choosing to exploratively approach low-percentage túngara calls) when presented with both a chorus playback and movement cue, further emphasizing the cognitive abilities of these bats. Given these conclusions, we encourage future research on how more cognitively complex animals deal with information complexity in varying decision-making contexts.

Author Contributions

Katie J. Galletta: Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Logan S. James:** Writing – review & editing, Writing – original draft, Software, Methodology, Formal analysis. **Dyess Harp:** Writing – review & editing, Writing – original draft, Investigation. **Kimberly L. Hunter:** Resources, Methodology, Funding acquisition, Conceptualization. **Ryan C. Taylor:** Resources, Methodology, Funding acquisition, Conceptualization. **Michael J. Ryan:** Writing – review & editing, Methodology, Funding acquisition, Conceptualization. **Rachel A. Page:** Writing – review & editing, Validation, Supervision, Resources, Project administration, Methodology, Funding acquisition, Conceptualization. **A. Leonie Baier:** Writing – review & editing, Writing – original draft, Validation, Supervision, Software, Project administration, Methodology, Funding acquisition, Conceptualization.

Data Availability

The data supporting the primary findings of this study as well as R code used in our reported analyses are included as Supplementary Material. All toolboxes and functions used are available on the MATLAB and R file exchange, respectively. Any additional materials are available upon request from the corresponding author.

Declaration of Interest

None.

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Supplementary Material

Supplementary material associated with this article is available at https://doi.org/10.1016/j.anbehav.2025.123318.

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