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Multimodal cues improve prey localization under complex environmental conditions

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Predators often eavesdrop on sexual displays of their prey. These displays can provide multimodal cues that aid predators, but the benefits in attending to them should depend on the environmental sensory conditions under which they forage. We assessed whether bats hunting for frogs use multimodal cues to locate their prey and whether their use varies with ambient conditions. We used a robotic set-up mimicking the sexual display of a male túngara frog (*Physalaemus pustulosus*) to test prey assessment by fringe-lipped bats (*Trachops cirrhosus*). These predatory bats primarily use sound of the frog's call to find their prey, but the bats also use echolocation cues returning from the frog's dynamically moving vocal sac. In the first experiment, we show that multimodal cues affect attack behaviour: bats made narrower flank attack angles on multimodal trials compared with unimodal trials during which they could only rely on the sound of the frog. In the second experiment, we explored the bat's use of prey cues in an acoustically more complex environment. Túngara frogs often form mixed-species choruses with other frogs, including the hourglass frog (*Dendropsophus ebraccatus*). Using a multi-speaker set-up, we tested bat approaches and attacks on the robofrog under three different levels of acoustic complexity: no calling *D. ebraccatus* males, two calling *D. ebraccatus* males and five *D. ebraccatus* males. We found that bats are more directional in their approach to the robofrog when more *D. ebraccatus* males were calling. Thus, bats seemed to benefit more from multimodal cues when confronted with increased levels of acoustic complexity in their foraging environments. Our data have important consequences for our understanding of the evolution of multimodal sexual displays as they reveal how environmental conditions can alter the natural selection pressures acting on them.

1. Introduction

Animals often use multimodal signals to attract mates and fend off rivals [1–3]. These multimodal signals can improve the detection, localization and discrimination of the sender's signal relative to simpler unimodal signals, and may sometimes increase the overall signal attractiveness [3–6]. However, eavesdroppers such as predators and parasites also attend to these displays and may often benefit in similar ways as intended receivers from attending to multimodal cues [7,8].

The perceptual benefits of multimodal cues for receivers probably depend on the environmental sensory conditions in which animals search for mates or hunt for prey [9–13]. Predators can be very efficient at using prey cues from single sensory modalities, such as mantis shrimps or dragonflies, which are highly specialized to hunt with their vision [14,15]. Many predators, however, hunt in environments in which the sensory conditions fluctuate widely over the day and across seasons. Under fluctuating environmental conditions, the use of multimodal cues might balance the increased cost associated with perceptual processing [12,13].

Multimodal cue use can be particularly useful when the perceptual conditions in one sensory modality become increasingly complex [11–13]. Males of some frog species that call near forest streams, for example, show elaborate foot-waving displays [16,17]. These displays are thought to have evolved in response to high levels of acoustic background noise to increase their detection

by prospective females. The underlying perceptual mechanism that may increase detection and/or localization when using multimodal cues under increased levels of environmental complexity, however, is still unclear [12]. For instance, acoustic noise can mask acoustic signals when overlapping in frequency [18–20]; adding visual signal components to a sexual display may reduce this masking impact [21]. Acoustic noise can also provide extra sensory information that, though irrelevant, nevertheless must be processed by an animal's brain [12]. Acoustic noise has been shown to grasp the attention or increase processing demand on animal perception [22–24] and under these conditions animals may benefit by switching to the use of cues from other sensory modalities [12].

The fringe-lipped bat (*Trachops cirrhosus*) is a predator that primarily relies on acoustic mating signals of frogs and insects to find its prey [25–28]. Once a prey sound is detected and approached, bats can use echolocation for further localization and chemical cues to assess prey palatability [25]. The túngara frog (*Physalaemus pustulosus*) is a preferred prey species of the fringe-lipped bat [28,29]. The male túngara frog can produce two types of calls: a simple call, consisting of a downward frequency sweep known as whine, or a complex call, consisting of a whine with one to seven amplitude-modulated pulses, or chucks, added to it [30]. Bats are better at locating the source of a complex caller and when given a choice prefer to attack speakers broadcasting complex calls to speakers broadcasting simple calls [31,32]. The male túngara frog also displays a large vocal sac that inflates with the call onset and deflates with call offset [33–35]. Bats have been shown to prefer a robotic frog model displaying a dynamically moving vocal sac coupled to sound playback over a control model [26]. Bats can detect vocal sac movements from their perch at a distance of at least 3 m using echolocation, but not vision [26]. Túngara frogs, on the other hand, are able to detect approaching bats under some conditions and exhibit evasive responses that vary with the perceived risk of attack [36].

In our first experiment, we tested how bats use multimodal cues during their approach and attack behaviour. We compared behavioural responses during robofrog trials (a dynamically moving vocal sac coupled in sync to sound playback) with responses during control trials (vocal sac movement perceptually inaccessible to the bat). We used both simple and complex calls to assess whether call complexity additionally altered approach or attack behaviour. In the second experiment, we tested whether the use of multimodal cues by bats changes under fluctuating environmental conditions (specifically, a mixed-species chorus). Túngara frogs often share breeding ponds with other frog species (mostly *Dendropsophus ebraccatus* at our study sites), and these noisy multi-species choruses can make it difficult for a bat to detect and/or locate its prey [32]. We exposed bats to our túngara robofrog while at the same time broadcasting calls from the hourglass frog (*D. ebraccatus*) from two or five nearby speakers allowing minimal temporal overlap with the túngara frog call.

2. Material and methods

(a) Study system

The study was carried out between January and May 2013 in Gamboa, Panama. Fringe-lipped bats (*T. cirrhosus*; $n = 9$) were captured with hand nets from known roosts in Soberanía National Park. Each bat was injected with a subcutaneous passive integrative transponder (Trovan Ltd.) for individual

recognition, and released in a large outdoor flight cage ($5 \times 5 \times 2.5$ m; see electronic supplementary material, figure S1, for layout). Bats were tested for up to five consecutive nights and released at their respective capture sites after the experiment.

(b) Robofrog presentation set-up

We used a robotic system to mimic a calling frog emitting either unimodal (acoustic cue only) or multimodal stimuli (acoustic cue plus vocal sac movement, known to be assessed by bats through echolocation). Our experimental set-up consisted of a frog model placed on a circular smooth-surfaced Plexiglas platform (\varnothing 30 cm; electronic supplementary material, figure S1). The platform was placed 10 cm above the ground, on top of a speaker (Peerless; 2.5 inch). The set-up contained a catheter (Rüsch latex 30 cc balloon) in front of the model (which mimicked the frog's vocal sac) as well as a catheter underneath the Plexiglas platform that functioned as a control for the sound produced by the inflation of the catheter (see [26] for details about this control condition). This control ensured that the bats' behaviour was not influenced by different sound production between the two experimental stimulus presentations. We drilled holes in the Plexiglas below the models to allow for sound transfer of the speaker and control catheter. Both catheters were connected with a 3 m tube to a custom-made gas-relay station driving the inflation and deflation of the system in synchrony with the call (see [26] for detailed description of the robotic set-up).

(c) Experimental design

Each bat was allowed one night to acclimatize to the flight cage and to the experimental set-up before trials began. Bats were given an $80 \text{ cm} \times 80 \text{ cm} \times 2$ m shelter made from black cloth attached to the ceiling of the cage; this shelter served as the bat's starting point for each experimental trial. The shelter was located in one corner of the experimental cage, open to the test set-up, which was situated 3–5 m away. We broadcast túngara frog calls in the absence of the robofrog with a few pieces of fish on top of the model frog as a reward for the bat. This ensured that the bats became acclimatized to the set-up and readily attacked models throughout the experiment.

The first experiment examined bat approach and attack behaviour on the robofrog. We used two different call types, either a synthetic simple call consisting of a whine or a synthetic complex call consisting of a whine plus one chuck (see [29] for details on synthetic call). Both call types were broadcast at one call per 2 s and at the average call amplitude of this species (76 dB SPL re. $20 \mu\text{Pa}$ at 1 m, measured with Extech SPL-meter type 407764, set to C-weighted, fast and max) from the speaker underneath the model. Sound playback was accompanied by presentation of the robofrog (inflation and deflation of a catheter in front of the frog model in synchrony with the sound) or control condition (inflation and deflation of a catheter underneath the frog model, concealed from detection by echolocation or vision by the bat). Playback of both stimuli was halted when the bat left the perch. We used a repeated measures factorial design with six replicates per combination of treatment levels, such that each bat had to complete 24 trials (two levels for robofrog stimulus, two levels for call type, six replicates). To keep motivation levels high, we rewarded half of the trials in a pseudo-random order. Furthermore, to keep bats motivated to search for the platform containing the reward from their perch, we added three dummy platforms to the test arena. The three dummy platforms together with the robofrog platform were randomly placed at one of 12 pre-determined positions in an arc-shaped grid (see electronic supplementary material, figure S1, for layout of the flight cage and platform locations).

The second experiment assessed bat behaviour under fluctuating acoustic conditions. We added two more platforms with

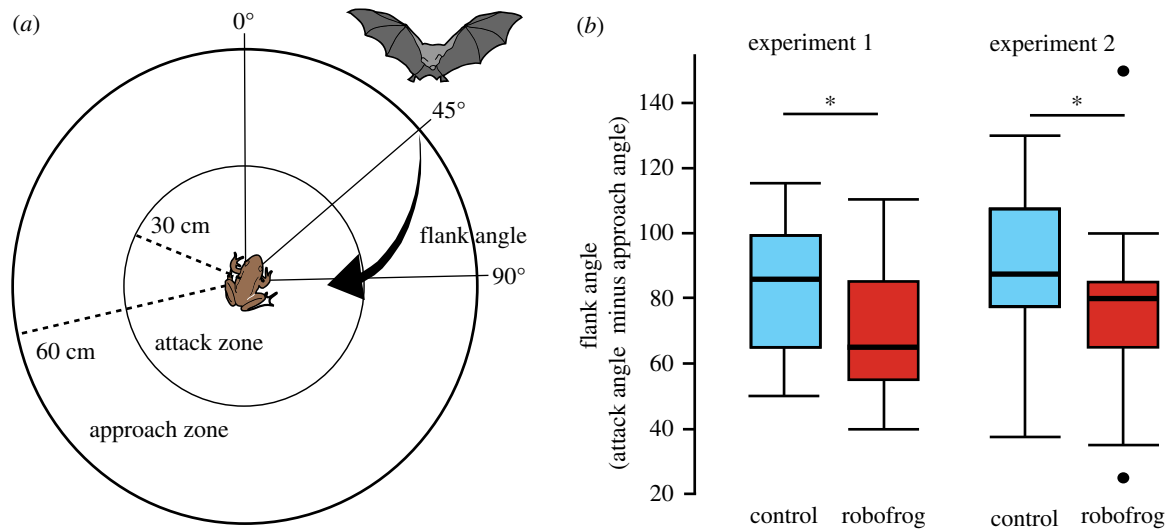


Figure 1. Robofrog presentation decreased flank attack angle of bats. (a) Robofrog set-up and zone of analyses. Shown are the frog model, a circular zone 60 cm from the model that we used to score approach angle, with 0° being the direction of the perch, and a circular zone at 30 cm from the perch that we used to score attack angle. Flank attack angle was defined as the differences in degrees between zone of approach and zone of attack, which is 45° (90 minus 45) in this example. (b) Median flank angles made by bats during experiment 1 and 2. Boxplots depict model estimates of fixed effect of the robofrog and show that bats make narrower flank angles during their attacks when the robofrog was present (red) compared to control conditions (blue). Stimulus presentation was switched off immediately after the bat left the perch (experiment 1) or after the bat entered the zone of attack (experiment 2). (Online version in colour.)

speakers to our test grid. The five dummy platforms were used to play calls from another species, the hourglass frog (*D. ebraccatus*), that often forms mixed-species choruses with tungara frogs. We tested bats under three different treatments: (1) no *D. ebraccatus* call, (2) *D. ebraccatus* calls played from two platforms, and (3) *D. ebraccatus* calls played from five platforms. Four of the dummy platforms were placed at the edges of the grid and a fifth platform was placed at the centre (electronic supplementary material, figure S1). The platform containing the robofrog was randomly repositioned between trials. For the *D. ebraccatus* playback, we used recordings from six different males recorded around Gamboa. For each *D. ebraccatus* male, we selected 9–17 high-quality recorded calls to construct a 1 min sound file with a call rate of one call per 2 s. Each sound file had a different start time and calls were therefore played sequentially, mimicking the natural calling behaviour of *D. ebraccatus*. Playback amplitude of *D. ebraccatus* was set to 76 dB SPL (which is lower than average, but within the natural range of this species [37]) to match tungara call playback and always started 30 s prior to playback of the robofrog set-up. All frog calls as well as the robofrog presentation were switched off after bats entered the attack zone. Bats may also prey on *D. ebraccatus*, but the dummy platforms were never rewarded and individuals that did make attacks on them quickly learned to avoid this. For this experiment, we also used a repeated-measures design, resulting in 36 trials (two levels for robofrog presentation, three levels for environmental complexity, six replicates). Location of the robofrog platform, trial order and *D. ebraccatus* soundfile were randomly assigned. All nine bats finished all of the trials in experiment 1 and eight bats finished all trials in experiment 2.

(d) Behavioural recordings

We used two camera set-ups to monitor and quantify bat behaviour during the experiments. A Sony Handicam (DCR SR45 camera) recorded the bats on the perch and a surveillance system (GeoVision GV-800B) was used to score approach and attack behaviour. Three different surveillance cameras were used. One placed underneath the perch recorded resting bats (Mini Video Audio 1/4" CCTV Camera Invisible 940 nm IR led 2.8 mm lens), one placed at the side of the flight cage recorded flight from perch to platform (HD mini 650TVL Sony CCD Effio-E DSP Color Video Camera), and one attached to

the ceiling recorded attack behaviour (mini 1/3" Sony CCD Pin-hole Camera). All cameras recorded with a temporal resolution of 29 fps under illumination of a 25 W transparent red Satco light bulb and a 12 W IR 100 Illuminator infrared lamp.

Prior to each test trial, a plastic screen with a radial pattern of electrical tape was centred on the robofrog platform. The screen was recorded from above with the wide-angle ceiling camera and was used to score the horizontal angle of approach as well as attack angle. The screen was divided in 24 compartments separated every 30° as well as by two zones (first zone of \varnothing 60 cm and second zone of \varnothing 30 cm). From the videos, we recorded which compartment the bats entered the first zone with their head (hereafter referred to as 'approach zone', with the compartment closest to the perch being 0° , see also figure 1a) as well as the second zone (referred to as 'attack zone'). We also scored latency to leave the perch after stimulus onset in seconds, as well as flight duration from perch to platform.

(e) Data analyses

Pilot experiments revealed high within- and between-individual variation in flight path. Consequently, bats approached and attacked models from all possible directions. To deal with the high levels of variation, we calculated two response variables to quantify approach and attack behaviour: (1) the variance in angles of approach at 60 cm from the frog model, hereafter referred to as 'approach directionality'; (2) the difference between angles of approach at 60 cm and angles of attack at 30 cm from the frog model, hereafter referred to as 'flank angle'. Additionally, we analysed (3) latency to flight and (4) flight duration. We calculated approach directionality by determining the length of the mean resultant vector (MRV) [38] of six angles of approach (six vectors with length 1) for each combination of treatments. The result was one data point on approach directionality per combination of treatments per bat that could take values between 0 and 1. Low approach directionality (MRV-length close to 0) effectively means that a bat approached the frog model from very different directions in six trials, whereas high approach directionality (MRV length close to 1) means that a bat approached the frog model six times from similar directions. Values of approach directionality were only comparable if they were computed from the same number of vectors [38], which was always the case.

We constructed linear mixed models using the package `lme4` in R v. 2.15.1 [39]. We determined the optimal random structure by fitting multiple mixed models with different random structures but the same fixed effects using REML, and selecting the one with the lowest corrected Akaike information criterion (AICc) value [40]. We used AICc rather than AIC because AICc penalizes the inclusion of extra parameters more strongly, thus preventing over-parametrization. We always allowed for random variation in the effect of explanatory parameters per individual bat by fitting random slopes as well as intercepts [40], unless this led to a substantial increase in AICc.

We used likelihood ratio tests between nested models, using ML, to find the optimal fixed structure [40]. Fixed effects included robofrog presentation, distance between perch and robofrog platform (averaged for analyses of approach directionality), call type (experiment 1) and number of calling *D. ebraccatus* (experiment 2). We visually checked the assumptions of the linear mixed model by inspecting a quantile–quantile plot of the residuals to check for normality and by plotting the residuals against the fitted values and each of the explanatory variables. Mixed models that showed non-normality, heteroscedasticity or non-random patterns in the residual spread were discarded.

Approach directionality data, as measured by MRV lengths, were bounded between 0 and 1, and skewed towards 1. The data were therefore arcsine-transformed to prevent violation of the linear model assumptions. Flank angle models showed severe deviations from normality in preliminary analyses due to a large number of extreme values. This problem did not disappear with transformations, so we averaged the data per combination of treatments per bat, resulting in a single data point per combination of treatments per bat. Latency to flight and flight duration were log-transformed to meet model assumptions. In both experiments, the optimal random structure of models with flank angle as response variable included bat identity as random intercept. The minimal adequate models with approach directionality as response variable included bat identity as random intercept, and a random slope per bat for the effect of vocal sac presence. For an overview of the response variables, optimal fixed and random effects used in each analysis, see electronic supplementary material, table S1. The assumption of normality was violated in models of experiment 1 with flight duration as response variable. Further transformations did not improve this. We did not analyse the flight duration for experiment 1 due to violations of model assumptions.

3. Results

(a) Experiment 1: use of unimodal versus multimodal cues

The presence of the robofrog with a dynamically moving vocal sac significantly affected flank angle. Bats attacked at an average flank angle of $70.5^\circ \pm 5.7$ (s.e.) when the robofrog was played and an angle of $84.1^\circ \pm 5.3$ (s.e.) under control playbacks (figure 1*b* and table 1). Túngara frog call type (simple or complex) did not have an effect on flank angle nor the interaction between call type and robofrog (table 1). Neither robofrog nor call type had an effect on approach directionality or latency to flight (table 1).

(b) Experiment 2: effect of acoustic complexity on multimodal cue use

The robofrog had a significant effect on the flank angle ($74.8^\circ \pm 5.8$ s.e. with vocal sac, $89.5^\circ \pm 6.1$ s.e. without vocal sac; table 1 and figure 1*b*). There was no effect of the number of calling *D. ebraccatus* on flank angle, nor was there an interaction effect (table 1). Approach directionality was significantly affected by the interaction between robofrog presentation and the number

of calling *D. ebraccatus* (table 1). The main effects of robofrog and number of calling *D. ebraccatus* were, however, small and insignificant (table 1). In other words, approach directionality only increased due to vocal sac presence when the number of calling *D. ebraccatus* was high (figure 2).

A *post hoc* model assessing the change in approach directionality due to the presence of the robofrog revealed an effect of the number of calling *D. ebraccatus* ($\chi^2 = 8.0$, d.f. = 2, $p = 0.018$), but only when played through five speakers (deviation from 0: $p < 0.01$; figure 2). The number of calling *D. ebraccatus* also significantly affected latency to flight: bats waited longer on their perch when more *D. ebraccatus* were played (table 1 and figure 3). The robofrog had a weakly significant effect on latency to flight, with bats leaving their perch more quickly when the vocal sac was dynamically displayed to them (table 1). The effect of distance from the perching position to the frog model was not significant, nor were any of the interaction effects. There was no effect of the robofrog or the number of calling *D. ebraccatus* on flight duration (table 1).

4. Discussion

We tested whether the presence of a multimodal cue affects the approach and attack behaviour of the fringe-lipped bat when hunting for túngara frogs. In the first experiment, we found that bats attacked with narrower flank angles with a dynamically inflating robofrog presented than with a non-inflating control. Narrower flank angles result in shorter flight paths, and thus less time spent between entering the approach zone and making the attack. In the first experiment, we halted stimulus presentation as soon as the bat left the perch. Therefore, narrower flank angles also suggest that bats are better at localizing their target from over 4 m away. In the second experiment, we tested whether an increasingly complex acoustic environment altered the behaviour of the bats and, in particular, their use of multimodal cues. We found that attack latencies increased exponentially with the number of *D. ebraccatus* calls broadcast. The presence of multimodal cues led to narrower flank angles with similar effect sizes compared with the first experiment. We also found an effect of stimulus playback on approach behaviour. Bats were more directional in their approaches when the dynamically inflating robofrog was present, but only during playback of *D. ebraccatus* calls. These results suggest that the use of multimodal cues improves localization performance of bats, specifically only under increased acoustic complexity.

(a) The use of multimodal cues from the predator's perspective

We found that in trials in which we increased the complexity of the acoustic scene bats took more time to leave their perch and make their attack. This suggests that bats had more difficulty detecting and/or localizing their prey using the passive acoustic cue of the frog's call. The calls of *D. ebraccatus* had little temporal and spectral overlap with the túngara frog call during our experiment. It is therefore likely that increased acoustic complexity distracts the bat rather than masks the túngara frog call. It has been hypothesized that animals should incorporate additional cues when information obtained from one cue becomes uncertain [11,41] and that cues that are received through different sensory systems are particularly useful to deal with environmental complexity [13]. We have previously shown that fringe-lipped bats echolocate from their perch in our robotic

Table 1. Likelihood ratio statistics (χ^2) and associated p -values for all fixed effects in the statistical models (calculated using ML). Model parameter estimates, standard errors and t -values are provided for fixed effects that were retained in the minimal adequate models (calculated using REML).

	response variable	fixed effect	χ^2	d.f.	p -value	model parameter	estimate	s.e.	t
experiment 1	flank angle	robofrog \times call type	2.62	1	0.107				
		call type	0.14	1	0.703				
		robofrog	5.32	1	0.021	intercept	84.14	5.31	15.86
						robofrog	-13.64	5.73	-2.38
	approach directionality (arcsine-transformed)	robofrog \times call type	2.16	1	0.142				
		robofrog	0.39	1	0.844				
		call type	2.33	1	0.127				
	latency to flight (log-transformed)	three-way interaction	0.2	2	0.903				
		robofrog \times call type \times distance							
		two-way interactions	4.45	5	0.486				
robofrog \times call type \times distance									
distance		0.57	2	0.754					
call type		1.83	1	0.176					
experiment 2	flank angle	robofrog \times number of calling <i>D. ebraccatus</i>	0.8	1	0.371				
		number of calling <i>D. ebraccatus</i>	1.59	1	0.207				
		robofrog	6.2	1	0.013	intercept	89.54	6.08	14.74
					robofrog	-14.79	5.78	-2.56	
	approach directionality (arcsine-transformed)	robofrog \times number of calling <i>D. ebraccatus</i>	5.93	1	0.015	intercept	0.949	0.081	11.72
						robofrog	0.021	0.104	0.20
						number of calling <i>D. ebraccatus</i>	-0.027	0.017	-1.55
						robofrog \times number of calling <i>D. ebraccatus</i>	0.061	0.025	2.47
	latency to flight (log-transformed)	three-way interaction	2.53	2	0.283				
		robofrog \times number of calling <i>D. ebraccatus</i> \times distance							
two-way interactions		4.77	5	0.445					
robofrog \times number of calling <i>D. ebraccatus</i> \times distance									
distance		0.82	2	0.665					
robofrog		3.91	1	0.048					
number of calling <i>D. ebraccatus</i>		10.41	1	0.001	intercept	1.041	0.392	2.66	
				robofrog	-0.289	0.146	-1.98		
				number of calling <i>D. ebraccatus</i>	0.116	0.036	3.24		
flight duration (log-transformed)	robofrog \times number of calling <i>D. ebraccatus</i>	0.03	1	0.87					
	robofrog	2.33	1	0.13					
	number of calling <i>D. ebraccatus</i>	1.3	1	0.25					

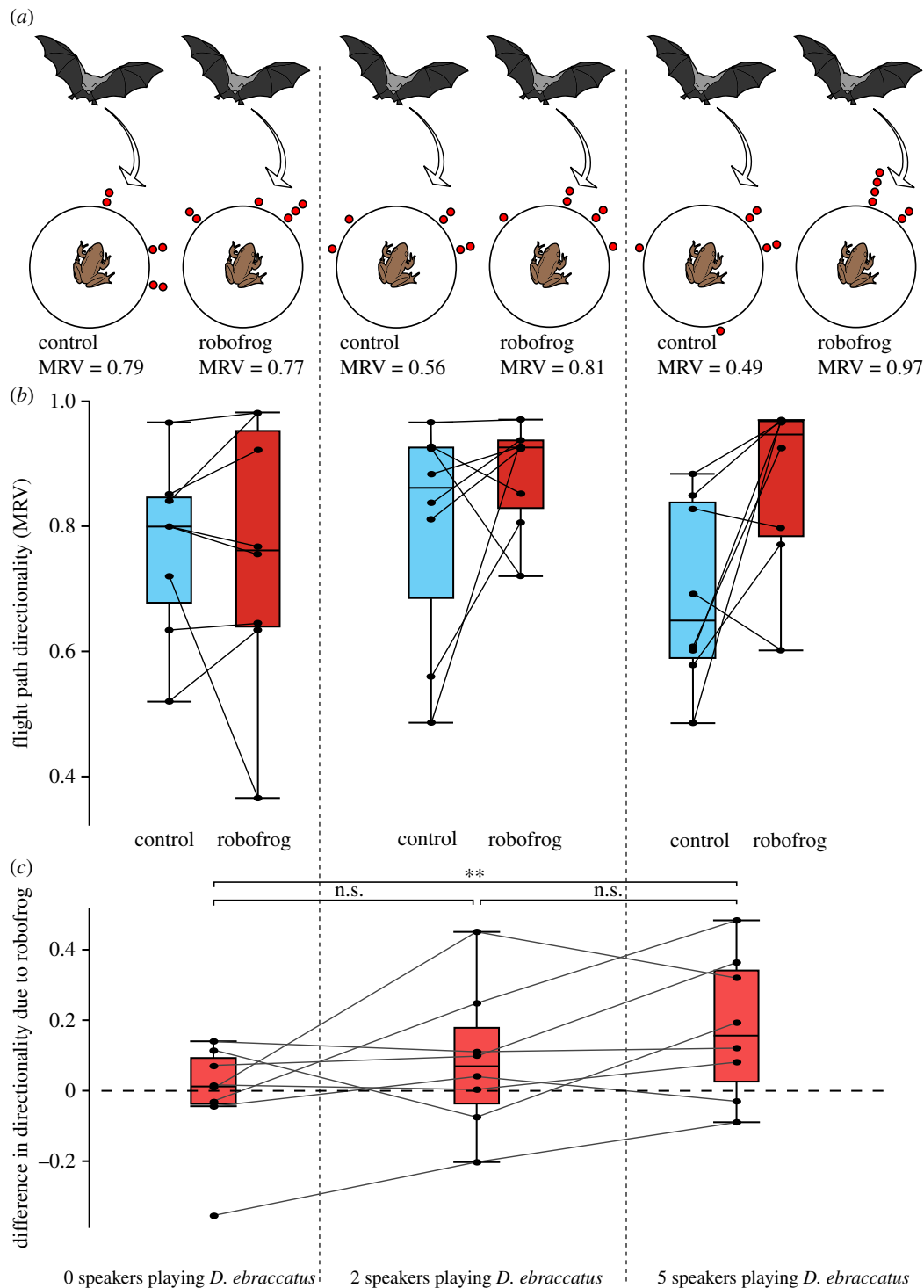


Figure 2. Multimodal cues increase approach directionality of bats under increased acoustic complexity. (a) Individual examples of the angles of approach made during the different experimental treatments. Each dot represents the compartment where a bat approached the frog model during a single trial. We show examples for trials with and without robofrog presentation as well as during trials in which either 0, 2 or 5 speaker platforms were playing *D. ebraccatus* male calls. For each bat, we assessed approach directionality by calculating the MRV length of all six trials from a treatment category. An MRV length of 1 indicates that a bat always approached from the same direction, whereas an MRV length of 0 indicates large variability in approach direction. (b) Approach directionality of all bats for all six treatments. Boxplots depict model estimates of fixed effects and lines indicate individual measures of approach directionality. (c) *Post hoc* model to illustrate the difference in directionality due to the robofrog under the three different *D. ebraccatus* treatments. The multimodal cue from the robofrog only altered approach directionality when five speakers broadcast *D. ebraccatus* calls. (Online version in colour.)

test set-up and that they can rely on multiple returning echoes from the moving vocal sac for prey assessment [26]. Spending more time on the perch when prey are calling allows bats to gather more echolocation information, and thereby improve their perceptual scene analyses [42,43].

We observed some additional interesting behaviour during our experiments that could provide more insight in the way

the fringe-lipped bat hunts. We noted that bats almost never approached the target in a straight line from perch to platform. Bats would typically enter the zone of approach from the flank or even back of the target platform and continue in a circular movement to make their attack. We have also observed these circular attack flights of bats during successful foraging attempts on live frogs. Male túngara frogs are able to visually detect

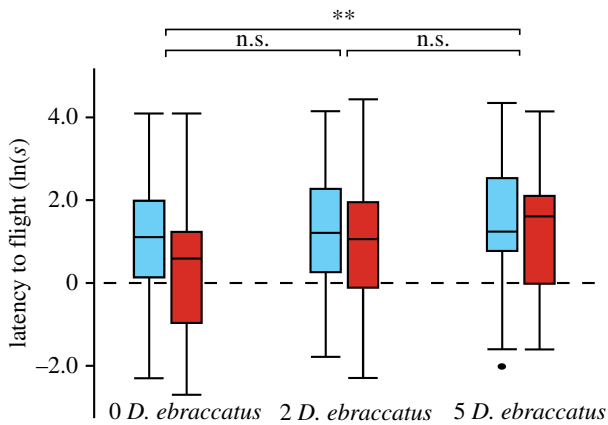


Figure 3. Increased flight latencies under increased acoustic complexity. Bats took longer to leave their perch and approach their prey when additional speakers broadcast *D. ebraccatus* calls. Boxplots are derived from model estimates for different *D. ebraccatus* treatments as well as robofrog treatment (robofrog in red, control in blue). The y-axis depicts natural log-transformed flight latencies. (Online version in colour.)

approaching bats and respond in a graded way in which they first cease calling, deflate and finally dive to the bottom of the puddle [36]. We would therefore expect bats to attack quickly. However, the circular attack flight could allow bats to position themselves in such a way that they can attack their prey from an optimal angle. The fringe-lipped bat also hunts for prey that can defend themselves, such as with toxins in frogs, for example, or large thorny mandibles in katydids [25,44]. Their circular flight may allow better identification and the ability to distinguish the potentially harmful front with harmless back of their prey. The use of multimodal cues at close range may also improve identification of palatability and optimal attack side, and allow for faster attacks.

(b) The use of multimodal cues from the prey's perspective

Bat predation has a profound impact on animal communication systems and can favour signalling in a chorus of conspecifics or heterospecifics [45–48]. Bats occasionally attack other species of frogs, and túngara frogs may therefore benefit from a dilution effect or the anti-predator behaviour of other frogs [49]. Our data also show that calling in a mixed-species chorus has a differential effect on signal components. Bats made more use of the multimodal cue in the mixed-species chorus. Thus, we would expect increased selection pressure from eavesdropping

predators on multimodal signals compared with unimodal signals under increased levels of sensory complexity.

Multimodal signals allow animals to shift energy between signal components when costs and benefits differ between communication channels [46,50]. Tropical katydids, for example, increase the use of substrate-borne vibrations at the expense of air-borne sounds under full moon light conditions [46]. This behaviour presumably evolved to allow private communication, and thereby avoid the risk of eavesdropping bats [46,51]. A calling túngara frog also induces water surface vibrations in addition to acoustic and visual cues [7,52]. Male frogs use this third communication channel during rival contests and can increase vibrational signalling with their legs [52–54]. Túngara frogs could thus shift energy towards the vibrational channel depending on environmental factors, such as increased acoustic complexity of a mixed-species chorus, but unfortunately this channel is not as private as one would think, as bats have also been shown to use water surface waves to find their anuran prey [7].

In summary, we have shown how predators can rely on multimodal prey-generated cues by testing fringe-lipped bats with robofrogs. Multimodal cues may aid bats in localizing their prey, particularly in a complex sensory environment represented by mixed-species frog choruses. Our data also provide insights as to why animals should rely on multimodal cues, as the relative costs and benefits of communication with separate sensory modalities can be context-dependent.

Ethics. All experiments with bats were licensed and approved by STRI (IACUC permit: 20100816, 1012, 16) and the Autoridad Nacional del Ambiente de Panamá (SE/A-6-11 and SE/A-94-11). All research reported here complied with IACUC protocols from the Smithsonian Tropical Research Institute. We obtained all required permits from the Government of Panamá.

Data accessibility. Raw data are available at the Dryad Data Repository: <http://dx.doi.org/10.5061/dryad.59t58>.

Authors' contributions. F.R. and W.H. designed the experiment. F.R. carried out the experiments. F.R. and W.H. analysed the data. R.C.T. designed the robofrog set-up. F.R., W.H., M.J.R. and R.A.P. discussed results, wrote the manuscript and contributed to revisions.

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