

RESEARCH ARTICLE

Acoustically eavesdropping bat predators take longer to capture katydid prey signalling in aggregation

Harish Prakash^{1,*}, Stefan Greif^{2,3}, Yossi Yovel^{2,3} and Rohini Balakrishnan¹

ABSTRACT

Prey that are signalling in aggregation become more conspicuous with increasing numbers and tend to attract more predators. Such grouping may, however, benefit prey by lowering the risk of being captured because of the predator's difficulty in targeting individuals. Previous studies have investigated anti-predatory benefits of prey aggregation using visual predators, but it is unclear whether such benefits are gained in an auditory context. We investigated whether katydids of the genus *Mecopoda* gain protection from their acoustically eavesdropping bat predator *Megaderma spasma* when calling in aggregation. In a choice experiment, bats approached calls of prey aggregations more often than those of prey calling alone, indicating that prey calling in aggregation are at higher risk. In prey capture tasks, however, the average time taken and the number of flight passes made by bats before capturing a katydid were significantly higher for prey calling in aggregation than when calling alone, indicating that prey face lower predation risk when calling in aggregation. Another common anti-predatory strategy, calling from within vegetation, increased the time taken by bats to capture katydids calling alone but did not increase the time taken to capture prey calling from aggregations. The increased time taken to capture prey calling in aggregation compared with solitary calling prey offers an escape opportunity, thus providing prey that signal acoustically in aggregations with anti-predatory benefits. For bats, greater detectability of calling prey aggregations is offset by lower foraging efficiency, and this trade-off may shape predator foraging strategies in natural environments.

KEY WORDS: Predator–prey, Calling prey aggregations, Katydid prey, *Mecopoda*, Lesser false vampire bat

INTRODUCTION

Prey receive numerous anti-predatory benefits through aggregation, including group vigilance, dilution of risk, reduced encounter of predators and predator confusion effect (Krause and Ruxton, 2002a). However, there are also costs associated with prey aggregation. Fish shoals get attacked more often by predators than individuals that are alone (Botham et al., 2005; Krause and Godin, 1995). In a terrestrial predator–prey system, wolves encountered and killed larger elk groups more than expected by chance based on availability (Hebblewhite and Pletscher, 2002). The increased risk has been attributed to prey aggregations being more conspicuous to

predators than lone individuals (Krause and Ruxton, 2002b). However, the risk due to increased attraction of predators to prey aggregations might be offset by the decreased capture success of a predator because of the difficulty in targeting a single prey when amongst conspecifics (Schradin, 2019). For example, capture success decreased for fish predators as prey shoal size increased (Ioannou et al., 2008; Krause and Godin, 1995) and peregrine falcons *Falco peregrinus* had lower success when attacking starling flocks *Sturnus vulgaris* as compared with singletons (Zoratto et al., 2010). Additionally, in experimental conditions, leopard geckos, *Eublepharis macularius*, and common marmosets, *Callithrix jacchus*, took longer to capture a mealworm in aggregates than when presented with a single mealworm (Schradin, 2000).

Previous studies on reduced predator foraging success when targeting prey aggregations have, however, predominantly been limited to predators that use visual cues for detecting prey (Jeschke and Tollrian, 2007). A recent review suggested that acoustically eavesdropping predators might be similarly affected by synchronously calling prey aggregations, but this requires empirical evidence (Goodale et al., 2019). In other words, it is not known whether eavesdropping predators can resolve the cocktail party effect, i.e. single out a calling prey in a chorus (Bee and Micheyl, 2008). As eavesdropping predators might face perceptual and cognitive challenges while locating an individual prey in a loud chorus (Page and Jones, 2016), the predator's foraging success is expected to decline when it attempts to capture prey in an aggregation as compared with a prey presented alone. However, the anti-predatory benefits that acoustically signalling prey may receive from aggregations have rarely been examined. In this study, we tested whether calling prey aggregations were preferentially approached by an acoustically eavesdropping predator but gained anti-predatory benefits through decreased capture success.

Predatory gleaning bats are interesting model systems to examine the effect of calling prey aggregations on predator foraging efficiency. Gleaning bats are known to eavesdrop on the mating calls of prey using passive acoustic cues (Jones et al., 2016; Schnitzler and Kalko, 2001). They also use echolocation, i.e. active acoustic cues to detect silent prey within vegetation clutter (Geipel et al., 2013). Previous studies have examined bat responses to prey aggregation and found contrasting results. The predation risk (number of prey captured in an hour) faced by the túngara frog, *Engystomops pustulosus*, from the frog-eating bat, *Trachops cirrhosus*, did not correlate with prey chorus size (Ryan et al., 1981). In another study, given the choice between two different prey group sizes, the frog-eating bat preferred the larger of the two (Hemingway et al., 2018). In contrast, the bat *Rhinolophus ferrumequinum* was not able to differentiate between choruses containing two or six individuals of a lekking moth species (Alem et al., 2011). Also, frog-eating bats approached unsynchronized frog calls broadcast through speakers more often than calls broadcast in synchrony (Legett et al., 2019; Tuttle and Ryan, 1982), suggesting that bats might face difficulties in localizing synchronously calling prey

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aggregations. Calling in synchrony also reduces the attractiveness of individual prey to eavesdropping predators (Legett et al., 2020). However, no previous study has tested whether prey signalling acoustically in aggregations decrease the capture success or capture efficiency of acoustically eavesdropping predators.

Gleaning bats combine passive eavesdropping for prey detection and localization with active echolocation for the actual attack. When using active echolocation, they face another challenge: segregating prey from background echoes. Bats face such a challenge from the echoes of vegetation clutter, which might mask the returning echoes of the prey. Mouse-eared bats took more time to deplete prey presented in a cluttered background of leaf litter (Arlettaz et al., 2001). In another study, the frog-eating bat's attack probability on water ripples (prey cue) in cluttered environments was found to be lower than in uncluttered environments (Halfwerk et al., 2014). Similarly, Daubenton's bat, *Myotis daubentonii*, caught fewer mealworms as the duckweed vegetation cover increased (Boonman et al., 1998). Prey could therefore use an alternative strategy of hiding within vegetation to reduce predation risk. We compared the effect of both strategies, calling in aggregation and hiding in vegetation clutter, on bat prey capture performance.

We hypothesized that calling insect prey would benefit from calling in aggregations and from calling in vegetation clutter, as both scenarios would increase the time taken for bat predators to capture individual prey. We further hypothesized that these two anti-predator strategies might have an additive effect. We emphasize that the possible anti-predatory benefits of these two strategies have not been directly compared before. From the predator's point of view, we hypothesized that they would preferentially approach calling prey aggregates, but that their short-term foraging efficiency in prey aggregates would be lower than if they approached solitary calling prey in the same foraging patch because of increased time taken to capture prey in aggregates.

We tested predator attraction to calling prey aggregations and examined whether katydid prey of the genus *Mecopoda* Serville 1831 face differential predation risk from the gleaning bat *Megaderma spasma* (Linnaeus 1758) (lesser false vampire bat) when calling in aggregation. Katydids of the genus *Mecopoda* aggregate and call in synchrony (Hartbauer et al., 2014; Nityananda and Balakrishnan, 2007, 2008). Nearly 60% of *M. spasma* diet comprises insects belonging to the order Orthoptera and the bat is known to use mating calls of katydids (family Tettigoniidae), including those of the genus *Mecopoda*, to detect and approach prey (Raghuram et al., 2015).

We first tested, using playback experiments, whether the bats showed a preference for aggregated over individual katydid calls. We predicted that bats would be attracted to synchronously calling prey aggregations as they are louder and more conspicuous than single calling prey. We then used prey capture tasks to test how bat foraging success and efficiency are affected by the strategy of prey calling in aggregation versus calling within vegetation clutter. For these tasks, our first prediction was that bats would take longer to capture individual prey in an aggregation of callers as compared with a single caller. Our second prediction was that the addition of vegetation clutter would increase the time taken for prey capture of both single and aggregated calling prey. We also examined the relative effects of prey aggregation and vegetation clutter on prey capture by the bats.

MATERIALS AND METHODS

Ethical clearance for carrying out this project was obtained from the Institutional Animal Ethics Committee (IAEC), Indian Institute of

Science (Project no. CAF/Ethics/519/2016). The study was conducted in Kadari Village, Udupi District, Karnataka, India (13°21'N–75°08'E) in the natural habitat of *M. spasma*. The behavioural experiments were carried out across 2 years (December 2017 to March 2019) in a flight cage made of steel wire mesh (6×6×2.75 m L×W×H) constructed outdoors. The cage was divided into two parts: one part (housing arena: 6×2×2.75 m L×W×H) housed the bat and the other part (experimental arena: 6×4×2.75 m L×W×H) was used for carrying out the experiments. A screen partition made of black cloth separated the two arenas and allowed control of bat entry into the experimental arena (see Fig. S1A for further details). The bats were caught in their roosts using locally prepared hand-held butterfly cloth nets, then released into the housing arena of the cage. The bats were fed with wild katydid prey captured locally and allowed to acclimatize to the arena on the first night. Trials were conducted on subsequent nights. Irrespective of the bat's performance, it was fed 2–3 prey at intervals of 60–90 min. On most occasions, only one bat was housed. On three occasions, when there were two bats in the cage, one bat was kept in a smaller enclosure inside the housing arena and fed while the other individual participated in the tasks. At no point did a bat have the opportunity to observe the other bat with which it was housed while trials were being conducted, thus ruling out social learning by observation. A large bowl of water was also provided in the housing arena. After completion of the experimental trials, the bats were fitted with necklaces of small, colour-coded wooden beads (to avoid pseudo-replication) and released back in the roosts in which they were caught (Garg et al., 2012).

A 4×2×0.15 m wooden frame was constructed in the experimental arena and placed on the ground (see Fig. S1A). This was divided into 16 parts for randomizing the positions of the speakers in the tasks (Fig. 1A). The speakers for carrying out the playback were placed under the frame and the whole set-up was covered with a thick black cloth. The prey offered as a reward for the experiments was immobilized by cooling just before the task and placed on top of this cloth directly above the speaker in natural standing position. Hereafter, this wooden frame with cloth will be referred to as the platform.

All experiments were video-recorded using three infrared dome cameras (Vivotek FD816B-HF2, 30 frames s⁻¹, 1920×1080). Two cameras together gave the view of the entire flight cage from the top: one was placed in the housing arena and the other in the experimental arena. The third camera was placed nearly 1 m above the ground such that it recorded the entry of the bat from the housing to the experimental arena, and recorded the bat localizing the prey on the platform. The katydid prey call was played back using ultrasound speakers (Ultrasonic Dynamic speaker ScanSpeak, with frequency range 1–120 kHz, Avisoft Bioacoustics) connected via an Ultrasound Gate (216H, Avisoft Bioacoustics) digital-to-analog converter to a laptop (Lenovo G560). The video recordings and audio playbacks were controlled via the laptop from the outside of the cage, ensuring that the bat's behaviour was not influenced by the experimenter while the bat was performing its tasks.

Testing preference for single versus aggregated calling prey

Bat preference for single or aggregated calling prey was tested in a choice paradigm using loudspeaker playbacks of prey calls (Fig. 1A). The 'Chirper' song type of the katydid genus *Mecopoda* (Fig. S2) was used for prey calls (Nityananda and Balakrishnan, 2006). The playback stimulus was a pre-recorded, natural chirp recorded in the laboratory at the Indian Institute of Science, Bangalore, in an anechoic room (Nityananda and Balakrishnan, 2006) using a

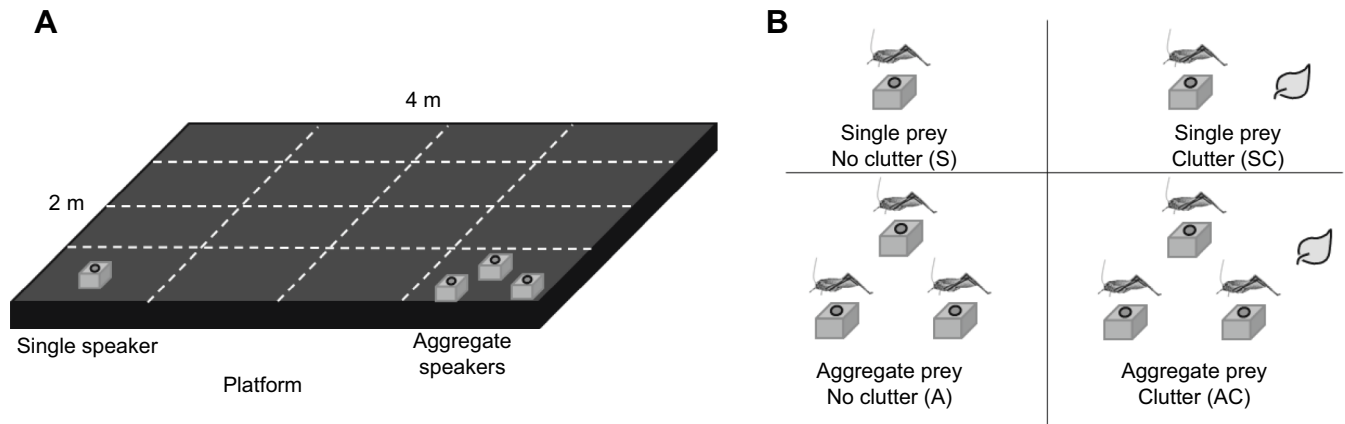


Fig. 1. Experimental design. (A) Design of the arena for the choice experiment between aggregate and single calls using speakers positioned as shown, under a black cloth. (B) Treatments for comparing prey capture.

Pettersson Elektronik D 989 Ultrasound Detector (custom-made microphone with a flat frequency response from 2 to 200 kHz). These recordings were digitized using a NI-DAQ AT-MIO-16E-2A/D card at a sampling rate of 200 kHz. Playback stimuli were not filtered. The pre-recorded natural chirp with mean chirp duration (109 ms) and typical spectrum (Fig. S2B) was played back at the mean call period (483 ms, with minor variations of up to 30 ms between successive individual chirp periods in a call) in a loop for 3 min. The call of this species as measured in natural populations consists of a series of stereo-typed chirps, with mean chirp period 483.3 ± 43.5 ms and mean chirp duration 109.2 ± 16.8 ms (Nityananda and Balakrishnan, 2006). Using one representative mean chirp pattern for playbacks rather than multiple natural variants has been argued to constitute pseudo-replication (Kroodsma et al., 2001). We argue, however, that, given the stereotyped nature of the *Mecopoda* 'Chirper' call and the normal distribution of call feature values, a mean pattern would be the most frequently encountered in the wild. Keeping the stimulus pattern consistent also increases the internal validity of our conclusions on the effects of aggregation and vegetation clutter on the efficiency of bat prey capture.

Katydid of the genus *Mecopoda* form part of the *M. spasma* diet and bats have previously been shown to respond to and approach playback of calls of *Mecopoda* species (Raghuram et al., 2015). The bat was offered the prey call choices at the two ends of the platform in the experimental arena, at least 2 m apart, with a single speaker broadcasting calls on one side, and three speakers (separated by 0.4 m from each other, arranged in an equilateral triangle) broadcasting simultaneously on the other, mimicking a natural synchronous chorus. The speakers were placed below the testing platform, which was covered with a cloth. The sound pressure level (SPL) of the single speaker was measured 0.5 m above the speaker (using a Bruel and Kjaer type 2250-S sound level meter) and ranged between 69 and 71 dB peak (re. 2×10^{-5} N m $^{-2}$). For the aggregation, the SPL was measured at the centroid of the three speakers, 0.5 m above the speakers. The overall SPL of the three speakers playing in synchrony was ~ 5 dB greater than that of the single speaker (Nityananda and Balakrishnan, 2009), with SPL settings of each of the single speakers being equal. The overall increased SPL mimicked the natural SPL levels of prey calling together in aggregation.

The experiment always began with the bat in the housing arena. After the call stimulus started, an entry point between the housing and experimental arena was created by opening the screen partition

and a ~ 1 m wide passage was created for the bat's entry. At the entry point, the two playback choices were equidistant to the bat. Prey calls were played from the speakers for 3 min continuously or until the bat approached. Whichever side the bat approached (~ 1 m away from the centre of the platform), containing either the single or aggregate calling speakers, was noted as its preference (see Movie 1). The approach behaviour of the bat was clearly distinguishable from flight behaviour without speaker playbacks. In playback trials, the bats flew close to the platform, approached the speaker side directly and on occasions were observed to slow their flight briefly over the playing speakers before flying past (see Movie 1). Unclear preferences in trials with a bat flying high above the platform or not choosing a side were discarded. The trial was carried out only once for each bat. The speaker positions under the platform for the preference test were constant (as shown in Fig. 1A); however, the side (left or right) from which the speaker choices were presented was interchanged for every bat ($N=19$). Note that bats were not trained before carrying out this task.

Prey capture under different treatments

Following the preference test, bats were trained to approach and capture the prey reward from the platform while the prey call (the 'Chirper' song type of the katydid genus *Mecopoda*) was being played out through the speaker directly below. As a reward for the bats, we used katydids belonging to the genus *Mecopoda* collected from the study area. Bats varied in the number of nights (1–3) they took to become trained. For 6 bats, the prey was tethered to a thread suspended approximately 0.5–1 m above the calling speaker. Once the bat approached the tethered prey associated with the call, the prey was placed on the platform and the call was played. For 8 bats, the prey was placed directly on the platform from the start. The training was complete once the bat successfully captured the prey on the platform when the call was played. It should be noted that bats had no difficulty localizing these single sound sources and approached them directly and hovered above or landed on the speaker on the first approach, i.e. they did not need to be trained to locate the sound sources, only to pick up the prey. The bats did not respond to every playback (3–5 min duration) trial and, on average, responded 2–3 times to the playback calls before they were successful in picking up the prey.

Following training, each bat was given eight experimental tasks with different treatments (Table 1) to complete within one or two nights. Unlike in the preference tests, either single or aggregated

Table 1. Tasks for prey localization

Task	Prey treatment	Clutter treatment	Call treatment	Code	Control/ experiment
1	Single	–	–	–	Control
2	Single	–	+	S	Experiment
3	Single	+	–	–	Control
4	Single	+	+	SC	Experiment
5	Aggregate	–	–	–	Control
6	Aggregate	–	+	A	Experiment
7	Aggregate	+	–	–	Control
8	Aggregate	+	+	AC	Experiment

Clutter treatment is indicated as with (+) and without (–) clutter. Call treatment is shown as without playback calls (–) for controls and with playback calls (+) for the experimental treatments.

prey were presented to the bat with or without vegetation clutter (Table 1 and Fig. 1B; Fig. S1B). The prey was kept immobile on the platform by cold treating it in a refrigerator just before carrying out the task. A chirp of mean duration and period from the ‘Chirper’ song type of the katydid genus *Mecopoda* was used as the call stimulus (Fig. S2). For acoustic complexity, the number of speakers broadcasting the katydid call was altered (one or three speakers). Corresponding to the number of speakers, the bats were presented either single (one prey item) or aggregate prey (three prey items spaced 0.4 m apart) placed directly above the speakers. For the aggregation treatment, multiple speakers (in this case three) broadcast the katydid call in synchrony to closely mimic the acoustic scenario of a natural chorus. The bat was thus confronted with the problem of locating and approaching one sound source among three closely spaced ones. Besides acoustic complexity, the habitat complexity was manipulated by either placing leaf litter on or removing it from the platform. The same amount of leaf litter (approximately 250 leaves) was sourced from the ground outside the flight cage and placed on the platform for all the tasks with habitat complexity. Moreover, care was taken to ensure that the leaf litter did not hide the prey on the platform, or obstruct the speakers playing the prey calls from beneath the platform (Fig. S1B).

Each task was a combination of prey type (single or aggregate) and clutter (with and without leaf litter) treatment (Fig. 1B). This combination was presented with (+) and without calls (–) (Table 1). The tasks with no calls lasted 15 min and served as a control to the tasks with calls (Table 1). The goal was to see whether bats could localize and capture prey without any sound cue. Each task was paired and presented with no call treatment first, followed by call treatment. Between the no call and call treatment, bats had to return to the housing arena. The order of presentation of these pairs – (1,2), (3,4), (5,6) and (7,8) – was randomized for each bat (see Table 1). Furthermore, the 16 positions (see Fig. 1A) available for presenting the speakers/prey on the platforms were also randomized between tasks for each bat. Each bat was tested once with each task. The variables measured for the tasks were whether the bat approached the presented prey on the platform, the time taken for the bats to capture the prey and the number of passes before the bat captured the prey (see Movie 2). Time to capture was calculated from the time of entry of the bat into the experimental arena to the bat capturing the prey with its mouth on the platform. The number of passes refers to the number of times the bat flew within a hemisphere of about 1 m diameter over the presented prey on the platform before prey capture. During the pass, the bats would fly about 1 m from the prey; other times, as close as a few centimetres. In general, these passes differed noticeably from the bat’s flight behaviour in the absence of speaker calls. Additionally, we also noted the number of landings

(the number of times the bat landed on the platform within 0.5 m of the prey) before successful prey capture.

For testing prey capture, 14 different bats were used. In total, there were 48 control tasks (with no sound cue) and 56 experimental tasks (with sound cue). Of the 56 experimental tasks, one task was discarded because of methodological error.

Statistical analysis

A binomial test was used to compare bat approaches to aggregated versus single calls in the preference test (see preference data in Dryad dataset: <https://doi.org/10.5061/dryad.pk0p2ngng>). The Friedman rank sum test was used to test whether responses to bat prey capture in treatments differed from each other. This was followed by pairwise comparisons with the Wilcoxon signed-rank test between responses to different prey capture tasks (see Dryad dataset: <https://doi.org/10.5061/dryad.pk0p2ngng>). Whether bats approached the prey directly or not during capture was compared between single and aggregated prey treatments using McNemar’s chi-squared test with continuity correction. These analyses were carried out in R software using the package ‘stats’ (<http://www.R-project.org/>).

Additionally, to compare between responses to treatments, a generalized linear mixed model (GLMM) with negative binomial error family was run with prey type (single and aggregate) and clutter (with and without), and their interaction as predictors (see prey capture dataset in Dryad: <https://doi.org/10.5061/dryad.pk0p2ngng>). The responses compared were time taken for the bat to capture the prey, and the number of passes the bat made before capture. Bat identity was included as a random effect. The analysis was carried out in R using the package GLMMadaptive (<https://CRAN.R-project.org/package=GLMMadaptive>).

RESULTS

Preference for aggregation

In 76% of cases (13 out of 17), bats preferred to approach aggregated prey calls over calls of single prey. Nineteen different bats were used for testing preference. Of these, 17 bats approached playback calls while two bats did not (see preference data in Dryad dataset: <https://doi.org/10.5061/dryad.pk0p2ngng>). Of the 17 bats that approached playback calls, 13 approached the side where aggregated calls were being broadcast while 4 approached the side with a single call (proportion of bats preferring aggregate calling speakers=0.764; binomial test two-sided, 95% confidence interval: 0.501–0.931, $P=0.049$).

Prey capture

Only once in the 48 control tasks (with no sound cue; see Table 1) did a bat capture an immobile prey (after 498 s), while in all 55 experimental tasks (with *Mecopoda* calls provided as the sound cue; see Table 1), bats ($n=14$) captured prey within 95 s. Hence, only prey capture in tasks with sound cues were used for further comparisons.

Overall, the time taken by the bats to capture prey as well as the number of passes were significantly different between the experimental tasks (Friedman rank sum test; time taken: $\chi^2=9.46$, $P=0.023$; number of passes: $\chi^2=14.896$, $P=0.0019$). Bats took on average nearly 10.56 s longer ($P=0.00085$) and made extra passes ($P=0.005$) before capturing prey in aggregation (as opposed to single calling prey) in the absence of vegetation clutter (A versus S; Fig. 2A,B). They also made an average of three passes over call aggregations compared with one pass for single callers in the presence of vegetation clutter (AC versus SC, $P=0.0094$; Fig. 2B). Vegetation clutter increased the average time taken to capture single

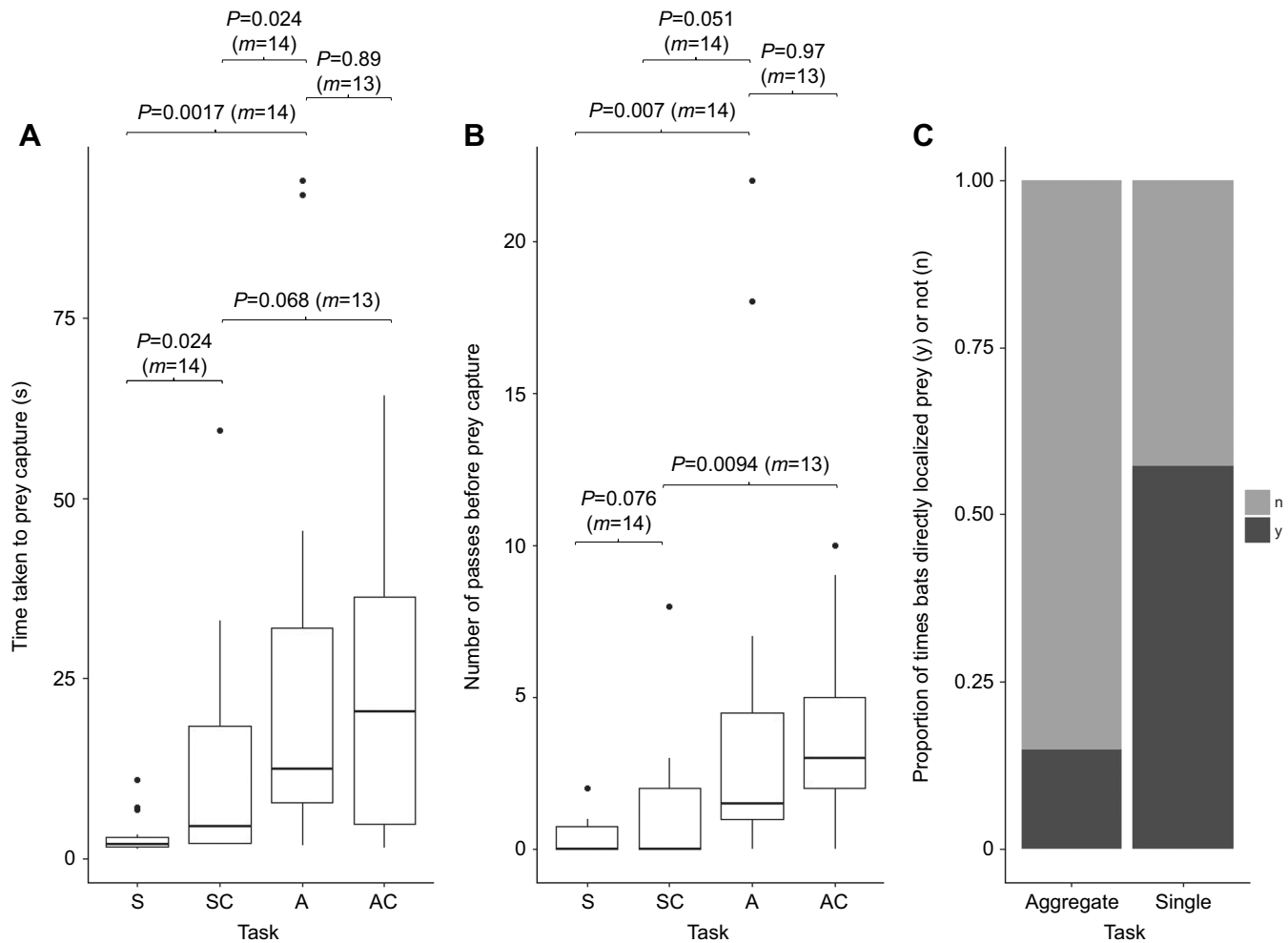


Fig. 2. Effect of call aggregation and vegetation clutter on bat prey capture. (A) Time taken to capture prey. (B) Number of passes before prey capture. Box plots show the median, upper and lower quartiles and $1.5\times$ the interquartile range; dots are outliers. P -values are from pairwise comparisons using Wilcoxon signed rank test. m is the number of paired samples compared between tasks. S, single prey; SC, single prey+clutter; A, aggregate prey; and AC, aggregate prey+clutter. (C) Proportion of times bats approached the prey directly in a task (y) or not (n). Comparisons were made using McNemar's test ($P=0.015$).

calling prey by 2.5 s (S versus SC, $P=0.024$; Fig. 2A) but did not significantly increase time to capture a prey in call aggregations (A versus AC, $P=0.89$; Fig. 2A). Additionally, average time taken to capture prey in aggregation (without vegetation clutter) increased by 8 s compared with that taken to capture calling single prey with clutter (A versus SC, $P=0.024$).

We also compared the number of times bats directly approached (number of passes=0 and bat landed accurately on the prey: y in Fig. 2C) or indirectly approached (number of passes>0 or bat crawled and reached the prey after landing: n in Fig. 2C) and captured prey for each treatment. Only in ~15% (4 out of 27) of trials involving prey aggregations (A and AC; Fig. 2C) did bats directly approach and capture a katydid. In contrast, bats directly approached and captured prey in ~57% (16 out of 28) trials involving single prey S and SC (Fig. 2C). Bats directly approached and captured single prey significantly more often than for aggregated prey (McNemar's chi-squared test with continuity correction; $\chi^2=5.88$, $P=0.015$).

Predicted values from GLMM (see Tables S1, S2 and S3) revealed that, in the absence of vegetation clutter, aggregation of calling prey increased average capture time of an individual caller by the bat predators by a factor of 7.1, whereas vegetation clutter

alone increased capture time by a factor of 3.2 (Fig. 3A; Table S1). Vegetation clutter did not add to the time taken to capture prey in call aggregations (Fig. 3A; Table S1). Similarly, in the absence of vegetation clutter, aggregation of callers increased the number of passes before capture by a factor of 12.2 compared with that for single callers (Fig. 3B; Table S3). In comparison, addition of vegetation clutter alone to single calls increased the number of passes 3.3-fold (Fig. 3B; Table S3). Thus, call aggregation increased capture time more than did vegetation clutter.

DISCUSSION

Acoustically signalling prey expose themselves to a high risk of bat predation (Page and Jones, 2016; Zuk and Kolluru, 1997). A common strategy for reducing this risk is signalling from within vegetation, which makes the prey much less conspicuous to detection by echolocation (Halfwerk et al., 2014). Here, we demonstrate that calling in aggregations can be as effective as calling in vegetation. Aggregate prey calls were preferentially approached by bats over single prey calls. However, the increase in time and number of passes before capturing prey in aggregations suggests that eavesdropping predators are challenged when trying to capture an individual prey within a calling aggregation. Taken together, these results suggest that

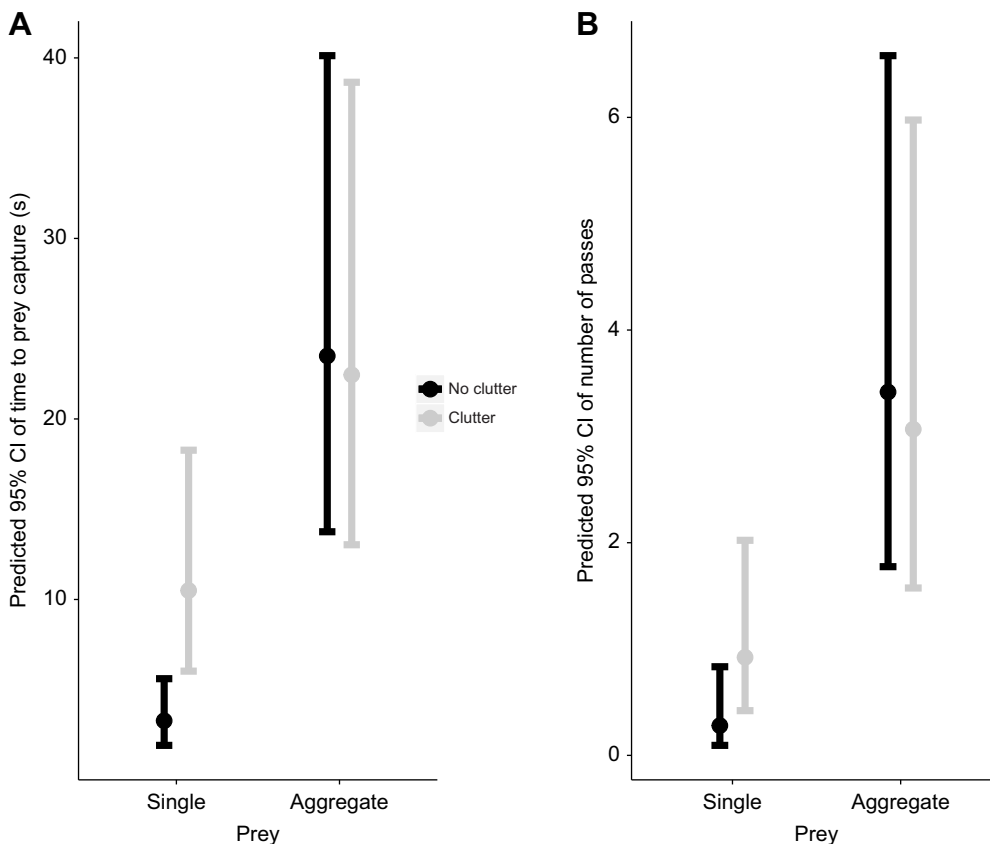


Fig. 3. GLMM model predictions for effect of call aggregation and vegetation clutter on bat prey capture. Data are the predicted 95% confidence interval (CI) values for (A) time to prey capture and (B) number of passes before prey capture.

though predators preferentially approach calling prey aggregations, they take longer to capture individuals within them. Interestingly, even though leaf litter (vegetation) did adversely delay the bat's prey capture, the effect was not as strong as that of prey aggregation.

Calling prey aggregations attract predators

Aggregated 'Chirper' calls of *Mecopoda* were preferentially approached by the bat predator, *M. spasma*. This preference for call aggregations is most likely a result of the increased loudness of the simultaneously broadcasting calls. For example, three or four *Mecopoda* calling in synchrony increase the overall sound amplitude by nearly 6 and 7 dB, respectively (Hartbauer et al., 2014; Nityananda and Balakrishnan, 2009), providing a louder auditory cue to eavesdropping predators as compared with a prey calling alone. Given the choice, the frog-eating bat, *Trachops cirrhosus*, was also attracted more towards louder frog calls (Tuttle and Ryan, 1981). This hints that eavesdropping predators probably prefer louder prey sources, including prey calling in aggregation. The predator could also be detecting prey calling in aggregation earlier, leading to the observed behavioural preference.

Predators, however, might not just use loudness as a cue for approaching prey aggregations. Complex calls of the túngara frog, *E. pustulosus*, are preferred as a cue by the frog-eating bat, *T. cirrhosus* (Ryan, 1985). The frogs tend to increase the proportion of complex calls when surrounded by neighbours, which might signal higher prey abundance to the bat predator (Bernal et al., 2007). Another study involving *T. cirrhosus* showed an overall preference for larger frog prey choruses than for smaller ones in a choice paradigm (Hemingway et al., 2018). The chorus call choices were presented through single speakers and were non-overlapping, and hence a larger chorus side would have a higher duty cycle as compared with the smaller one (Hemingway et al., 2018), which in turn might signal a larger prey

patch for the bat predator. In summary, calling prey aggregations are preferentially approached by bats, but the call properties that signal prey aggregations to the predator might differ and could consist of loudness, complexity and/or duty cycle.

Prey capture in the absence of prey-generated calls

The near absence of prey capture by *M. spasma* in control tasks (with no sound cue) indicates that prey-generated sound cues might be necessary for detection and capture of prey on substrates. This corroborates previous predictions that substrate-gleaning bats similar to *M. spasma* might rely more on prey-generated sound for prey detection at long range (Denzinger and Schnitzler, 2013; Page and Jones, 2016; Schnitzler et al., 2003). However, this does not rule out the possibility that *M. spasma* might be able to locate motionless or moving prey using echolocation, similar to other gleaning bats such as *Megaderma lyra* (Marimuthu, 1995; Ratcliffe et al., 2005; Schmidt et al., 2000) and *Micronycteris microtis* (Geipel et al., 2013, 2020). Echolocation could help them at close range before prey capture if the situation is favourable through suitably positioned prey or oblique approach angles (Geipel et al., 2019; Taub and Yovel, 2020).

Prey capture in calling aggregations and the confusion effect

In this study, single prey were either approached directly by bats or fewer passes were taken before capture than tasks with aggregated prey. This decrease in capture efficiency of the eavesdropping predator in response to calling prey aggregations is similar to what visual predators face when targeting a prey amongst its conspecifics. In the visual context, Schradin (2000) found that leopard geckos changed their head position more often before capture when presented with multiple mealworms as prey as compared with a single mealworm. The increased time taken by visual predators to

catch prey in aggregations was attributed to a ‘confusion effect’, which is the difficulty predators face when attempting to capture individual prey surrounded by other conspecifics (Schradin, 2000). Similarly, in this study, the increased time taken for capturing a prey in acoustically signalling aggregations by an eavesdropping predator suggests a confusion effect in the auditory context. To the best of our knowledge, this is the first study that demonstrates that multiple individuals signalling acoustically together can confuse their eavesdropping predator.

The mechanistic reason for the bat’s delayed time to capture of prey in aggregation might be explained by multiple factors. Locating one sound source among many simultaneously presented similar ones, as happens in a signalling aggregation, might be a challenging auditory localization problem for a bat, especially when the passive sound cues are similar in loudness, close together in space and in synchrony (Bee and Micheyl, 2008; Goodale et al., 2019). This could be the reason for the preference for unsynchronized prey calls by frog-eating bats (Legett et al., 2019; Tuttle and Ryan, 1982). Another reason could be on a more cognitive level: the bat is drawn in by the aggregated calling, but then has to first decide on one of the sources and then localize it, akin to the paradox of choice (Schwartz, 2004). In other words, the bats might have no difficulty locating the different sound sources (calling prey) but their indecisiveness in making a choice among them may be observed as delayed prey capture.

At close quarters, the bat’s active localization using echolocation might be affected by the masking of echoes it receives from multiple prey and/or leaf litter. We recorded the echolocation of *M. spasma* using an ultrasound detector (Pettersson D1000X) to confirm that they were echolocating during the prey localization, but we did not record consistently to compare echolocation between conditions. It has been shown that bats are able to weigh different cues from prey using both active and passive listening sensory modalities to locate prey (Gomes et al., 2016). It is possible that the challenge of using both passive and active listening together delays the predator’s prey localization (Barber et al., 2003). Future studies will examine what aspects of the bat’s auditory information processing, in active and/or passive sound localization, are affected when the bat attacks prey in calling aggregations.

One possible caveat of this study is using one representative chirp of the *Mecopoda* ‘Chirper’ (katydid) call with mean duration and mean period as a stimulus for all our experiments instead of different exemplars of the chirps to capture natural variation in chirp properties (Kroodsma et al., 2001). However, given the stereotyped nature of the *Mecopoda* ‘Chirper’ call, which consists of only a single chirp type, the relatively low variation in call properties (Nityananda and Balakrishnan, 2006), and the normal distribution of values of different call features, we believe that using a representative mean call that remained constant across treatments is valid and improves the internal validity of our conclusions. It is, however, important to include the natural variation in call temporal features to extend the external validity of our conclusions and this will be incorporated in future experiments.

Protective benefits of calling in aggregation versus calling from vegetation

In this study, vegetation clutter increased the time taken for approach and capture of prey in tasks involving single prey. This could indicate that bats do use echolocation when approaching a prey item. Either it is used for prey localization in the very last moments before capture or it is used to control the general approach to a surface. Further experiments are required to test these possibilities. In

contrast, vegetation clutter did not change prey capture time in tasks involving prey aggregations. This indicates that localizing prey in aggregation might already be a difficult task and vegetation clutter did not add significantly to the predator’s capture time.

No previous study has compared the protective benefit of aggregation with vegetation clutter for the prey. In this study, both prey aggregation and vegetation offered protective benefits for the calling prey by delaying the predator’s time to capture. However, the predator’s greater delay in prey capture in aggregations, even in the absence of vegetation clutter, suggests that calling in aggregation might offer more or as much protection to prey as calling alone within vegetation. This might be one reason for prey to signal next to a neighbour, even though signalling together tends to attract more predators and also results in greater competition for mates. However, the protective anti-predatory benefit that prey receive from vegetation clutter needs to be examined further, as vegetation clutter in the natural environment can be much denser than presented in our experiments and an increase in the structural complexity of vegetation might provide additional protection for the prey.

Consequences for the predator and prey

One could argue that the outcome of prey capture for the predator was not different as the bats were able to eventually capture one katydid in all the experimental conditions when prey were calling. The predator even appeared to resolve the cocktail party effect of singling out a prey from its chorus. However, it is to be noted that the playback calls of the prey continued to play when the bat approached, and the katydids were kept immobile, allowing the predator to make its capture. In nature, calling prey are likely to respond to bat approaches (ter Hofstede et al., 2010) and to conspecifics calling nearby. The time delay of the predator’s decision to make a prey capture attempt will allow a window of opportunity for the prey to take evasive action and escape by hiding in the undergrowth or falling silent (Symes et al., 2016) and so bring down the per capita risk of predation. Additionally, individuals in prey aggregations might respond to their neighbours and stop calling, which further decreases prey detectability by predators. All these might further decrease the foraging efficiency of an eavesdropping predator when attacking calling prey aggregations under natural conditions.

From a bat’s perspective, prey aggregation increases detectability from longer distances, but its foraging efficiency is lowered when attacking calling aggregations. This trade-off between detectability and capture efficiency may determine bat foraging strategies in natural environments. From an optimal foraging viewpoint, the increased search time is disadvantageous, but the benefits the predator might gain by hanging around prey aggregations for longer times might still outweigh the costs. The prey is comparatively large and nutritious, and the chance of catching one of these aggregated insects may be increased compared with a single prey item. Future studies will examine the effects of these trade-offs on bat foraging strategies.

From the prey’s point of view, the lowered predation risk of calling in aggregation may be a strong selection force for both aggregation and synchronous calling (Nityananda and Balakrishnan, 2009). The results of this study also suggest that calling in an aggregation might provide more or as much benefit to individual prey as the refuge of vegetation clutter.

Acknowledgements

We thank Sudhakar Gowda for assistance in the field, Hanumanthan Raghuram for advice on how to maintain and carry out behavioural experiments with bats in flight

cages, and Kavita Isvaran for advice on data analysis. We also thank the reviewers for their careful reading and constructive criticism, which much improved the manuscript.

Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: H.P., R.B.; Methodology: H.P., S.G., Y.Y., R.B.; Validation: H.P.; Formal analysis: H.P.; Investigation: H.P.; Resources: R.B.; Data curation: H.P.; Writing - original draft: H.P.; Writing - review & editing: S.G., Y.Y., R.B.; Visualization: H.P.; Supervision: R.B.; Project administration: H.P.; Funding acquisition: R.B.

Funding

This project was supported by funds from the DBT-IISc Partnership Program (Phase II; Department of Biotechnology, Ministry of Science and Technology, India; grant number BT/PR27952/INF/22/212/2018), for fieldwork and consumables. Equipment used in the study was funded by the DST-FIST [Department of Science and Technology, Ministry of Science and Technology, India; sanction number SR/FST/LSII-025/2009(C)] and DST-SERB (Department of Science and Technology, Ministry of Science and Technology, India; grant number EMR/2016/002293) to R.B. The Ministry of Human Resource Development (MHRD), Government of India funded H.P.'s fellowship and Tata Trusts Travel Grant, IISc, supported his travel for an international conference to present preliminary results.

Data availability

Data are available from the Dryad digital repository (Prakash et al., 2021): dryad.pk0p2ngng

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Cage setup

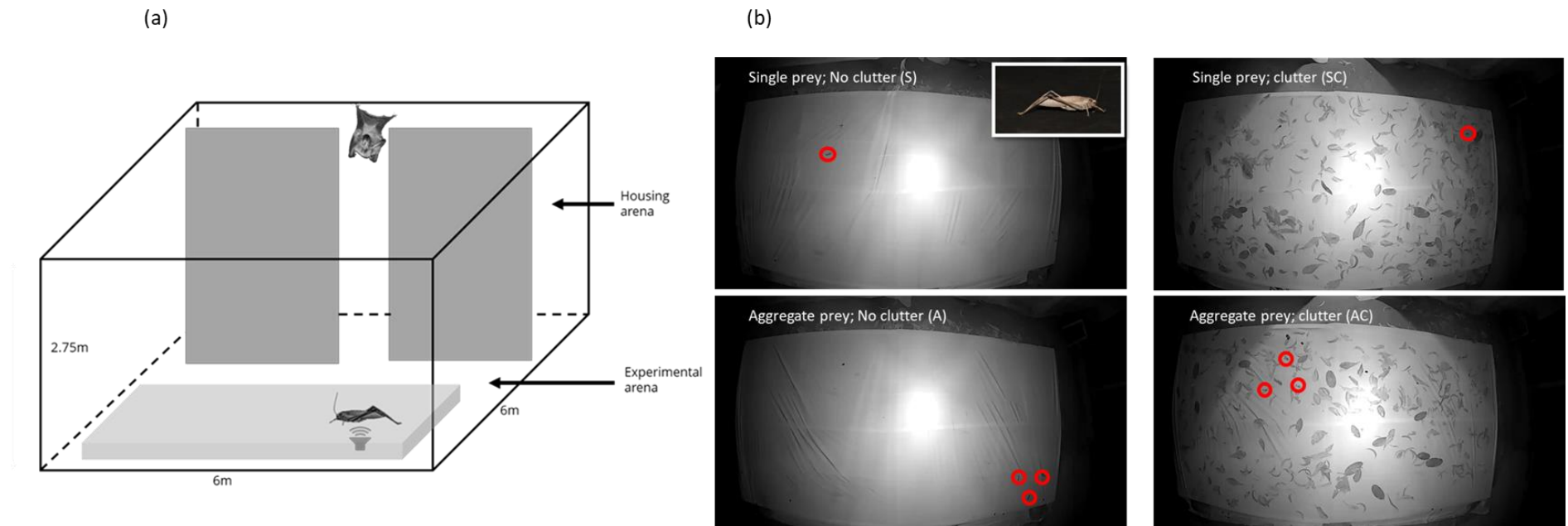


Fig S1. (a) Schematic of the flight cage. (b) Platform setup (top view) in the experimental area of different treatments. Red circles indicate prey positions (locations were changed randomly between tasks). Inset is the image of immobile prey, *Mecopoda*.

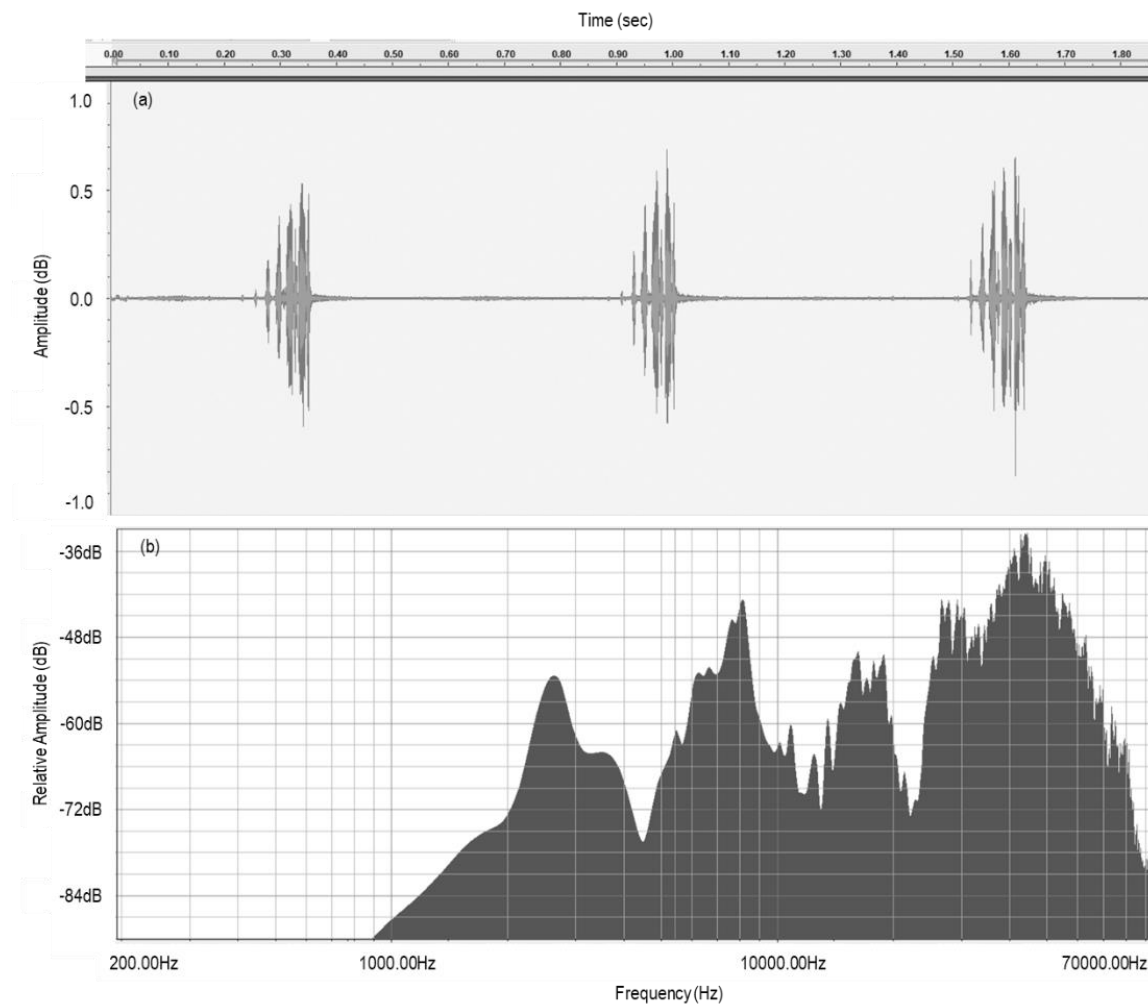


Fig S2. (a) Oscillogram and (b) power spectrum of 'Chirper' song type of the katydid *Mecopoda*. Chirp duration = 109 milliseconds; Chirp period = 483 milliseconds.

Fixed effect estimates of the Generalised linear mixed effect models (GLMM) for time to capture prey and number of passes before prey capture

Table S1. Fixed effect estimates from GLMM, their standard error, z-value and p-value for time taken to prey capture. The baseline predictor (intercept) against which other predictors were compared against was, single prey in a no clutter environment, referred as prey_single. prey_aggregate refers to the effect of prey aggregation, and clutter_clutter refers to the effect of clutter on the response. Finally, prey_aggregate:clutter_clutter refers to the interaction between both the predictors (prey type and clutter type) and how it affects the responses. The predicted values and their 95% confidence intervals were extracted from estimate outputs of the models.

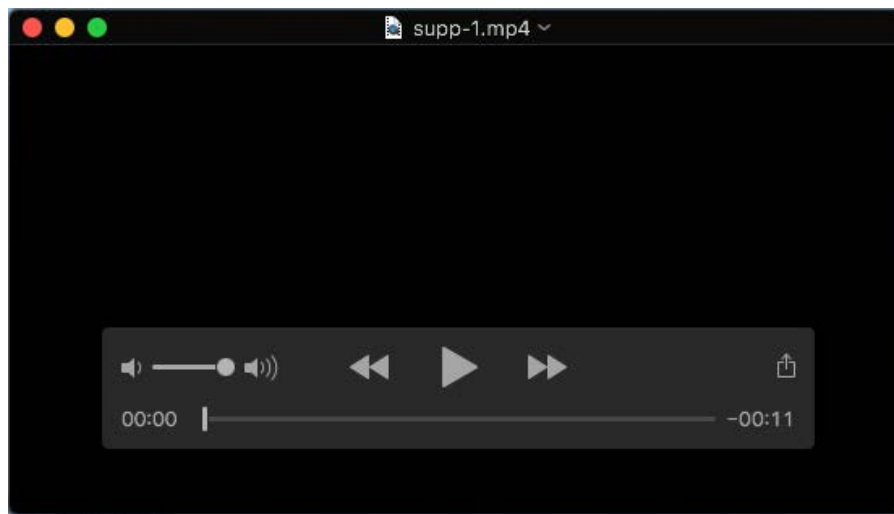
	Estimate	Std.Err	z-value	p-value
prey_single (Intercept)	8.096	0.274	29.570	< 0.0001
prey_aggregate	1.968	0.362	5.433	< 0.0001
clutter_clutter	1.163	0.369	3.152	0.0016
prey_aggregate:clutter_clutter	-1.208	0.518	-2.332	0.0197

Table S2. Fixed effect estimates from GLMM, their standard error, z-value and p-value for number of passes before prey capture.

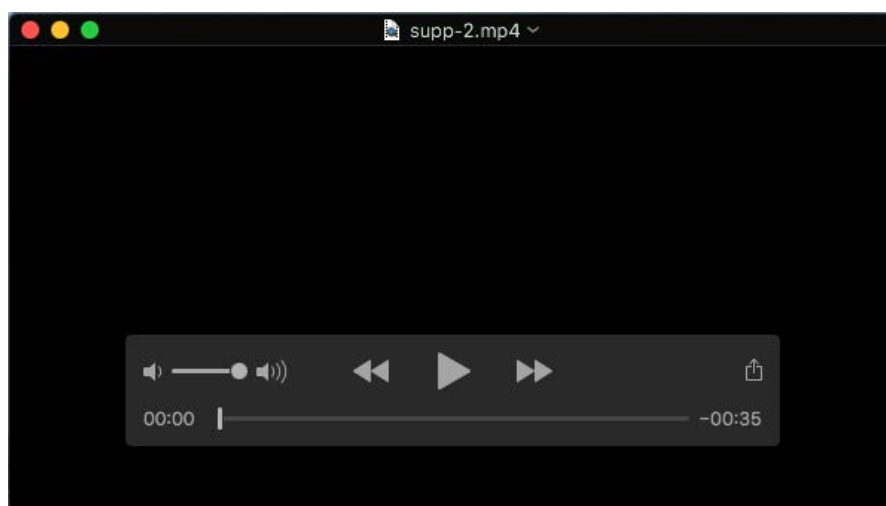
	Estimate	Std.Err	z-value	p-value
prey_single (Intercept)	-1.273	0.557	-2.286	0.0222
prey_aggregate	2.502	0.570	4.388	< 0.0001
clutter_clutter	1.192	0.602	1.979	0.0478
prey_aggregate:clutter_clutter	-1.3	0.704	-1.848	0.0646

Table S3. Factor increase comparison between tasks from predicted average values of GLMM. For example, capture time increases by a factor of 7.12 for A (aggregated prey + no clutter) in comparison to S (single prey + no clutter) and the number of passes increases by a factor of 12.3. SC (single prey + clutter), AC (Aggregate prey + clutter).

Pairwise comparison of tasks	Factor increase in time taken	Factor increase in number of passes
S-A	7.15	12.2
S-SC	3.2	3.29
S-AC	6.84	10.96
SC-A	2.24	3.71
SC-AC	2.14	3.33
AC-A	1.05	1.11



Movie 1. Single vs. Aggregation. Example of predator approach in choice experiment. Single speaker (Left) vs. aggregated speakers (Right)



Movie 2. Prey capture tasks. Example of prey capture in two different treatments. Treatment 1. Single prey + no clutter (S) and Treatment 2. Aggregate prey + clutter (A)