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Snake-like bird hisses induce anti-predator responses in a frog

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Abstract

Some snakes emit hissing calls which are imitated by birds to deter potential predators. However, the effect of these snake and bird hisses on anuran risk recognition is not yet explored. Here we hypothesize that these hisses may advertise dangers to frogs and evoke their anti-predator responses. We used little torrent frogs (*Amolops torrentis*) as subjects and conducted sound playbacks to test their anti-predator behaviors. We found that little torrent frogs changed their calling behaviors during sympatric snake hiss playbacks, but showed no response to white noise and allopatric snake hiss playbacks. They did not respond to sympatric avian hiss that has low acoustic similarity with snake sounds. However, they decreased calling activity in response to sympatric avian hiss that has high acoustic similarity with snakes. As compared to other treatments, more individuals ceased calling during the playbacks of the highly similar bird hiss. These results suggest that frogs may recognize risks from snake and snake-like hissing calls and perform anti-predator responses.

Keywords Anti-predator response, Hissing call, Sound playback, Vocal mimicry, Zitting cisticola

Acoustic signals are widely used for conspecific communications in animal kingdom. However, animals also transmit information to unintended audiences when they perform calling behaviors (Phelps et al. 2007; Aschemeier and Maher 2011; Halfwerk et al. 2014; Liu and Liang 2022). Acoustic heterospecifc eavesdropping is an interesting research topic in animal behavior and ecology field. For those unintended receivers, eavesdropping on the information of other taxa can reduce uncertainty and makes optimal decisions (Page and Ryan 2008; Akre et al. 2011; Magrath et al. 2015). Eavesdropping on heterospecific vocal signals has a close relationship with diverse contexts such as prey/host detection, predator avoidance, mate choice, and resource defense (Danchin et al. 2004; Magrath et al. 2015; Goodale et al. 2019; Bernal and Page 2023).

As compared to conspecific eavesdropping alone, heterospecific eavesdropping has a potential to gain more information across various taxa (Phelps et al. 2007; Magrath et al. 2015). Studies of frog-biting insects suggest that midges have evolved an ability of eavesdropping on anuran advertisement calls and use the calls to locate their hosts (de Silva et al. 2015; Legett et al. 2019; Zhao et al. 2022b). Such interspecific interactions bring longer-term foraging benefits and could promote the appearance of species-specific innate responses (de Silva et al. 2015). Some reptiles, birds, and mammals are found to exploit heterospecific alarm calls to obtain immediate anti-predator benefits (Magrath et al. 2015). For instance, wild capuchin monkeys (*Sapajus nigritus*) perform adaptive anti-predator reactions after learning to associate heterospecifc alarm signals with predators (Wheeler et al. 2019). Studies of forest reptiles and birds show that iguanas can discriminate mobbing calls of sympatric flycatchers from other calls and then increase their vigilance

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behaviors (Ito and Mori 2010). Anura (frog and toad) is one of the main taxa that communicate with sound signal. However, heterospecific acoustic eavesdropping is largely unexplored in anuran species.

Some anurans are able to detect predators by conspecific alarm or distress calls (Forti et al. 2017; Hopkins and Folt 2019). For instance, smoky jungle frogs (*Leptodactylus savagei*) are warned by scream calls of nearby conspecific individuals during predation events (Hopkins and Folt 2019). Studies of túngara frogs (*Physalaemus pustulosus*) indicate that anurans can selectively attend to heterospecific frog calls produced in presence of predators and may regard choruses as alarm signals (Phelps et al. 2007; Dapper et al. 2011). Moreover, anurans may make a trade-off between reproductive benefits and survival costs when they recognize the change of risks. When túngara frogs produce complex calls to attract females, they also have attractiveness to predators and parasites (Bernal et al. 2006; Akre et al. 2011; Halfwerk et al. 2014). The túngara frogs from urban population not only detect a change in predation and parasitism pressure from eavesdroppers, but also show adaptive signaling adjustments in forest vs. urban sites (Halfwerk et al. 2019). Some anuran predators (e.g., birds and snakes) also emit sounds (Aubret and Mangin 2014; Møller et al. 2021b), which is likely to advertise risk information. Few studies have tested whether anuran species can exploit predator calls to avoid enemies (but see Phelps et al. 2007).

Snakes are one of the main predators of frogs. Despite having a weak hearing ability, they can generate sounds in various ways (Young 2003). When threatened, some snakes generate highly defensive hissing calls. The hisses have similar spectral traits with poor structure (Young et al. 1999; Aubret and Mangin 2014). Such sounds may not indicate one-to-one links between alarm signals and predators (or predator contexts) tightly, which could promote the achievement of risk recognition by receivers (Price et al. 2015; Deshpande et al. 2023). Recently, some birds are found to mimic the hisses of vipers to deter potential predators (reviewed by Møller et al. 2021b). The hisses can influence avian reproductive success (Koosa and Tilgar 2016) or increase its chances of escaping from predators (Krams et al. 2014; Zub et al. 2017). To our knowledge, however, so far no research has tested whether these hisses advertise dangers and induce anti-predator responses in anuran species.

Snake's hisses show a high degree of similarity, although their acoustic durations may vary in different species (Young 2003). These hisses have a low acoustic specialization and may provide broad warning signals (Møller et al. 2021b). Meanwhile, the high degree of similarity between snake and bird hisses has also been revealed in sympatric (e.g., Dutour et al. 2020) and allopatric species (e.g., Møller et al. 2021a). Therefore, frogs may react to hissing sounds from snake predators. However, the hiss is only emitted by a snake when it is threatened (Møller et al. 2021a). Given that snakes eat frogs it is unlikely the hiss is emitted during a hunting sequence. Therefore, if it is a sound in the context of eavesdropping on an alarm signal then the frogs could be cuing in on a sound that indicates a predatory threat that is shared among snakes, birds and the frogs. We thus presume that snake and avian hisses may evoke anti-predator responses in a similar manner.

Here we used little torrent frogs (*Amolops torrentis*) to test our hypothesis. This species emits loud and long (~5.5 s) calls consisting of many short notes (Zhao et al. 2018). Males often perform calling behaviors throughout the entire day and night consequently, overlap in the active periods of sympatric snakes and birds. Hainan Island is a common distribution area of little torrent frogs, zitting cisticolas (*Cisticola juncidis*) and cinereus tits (*Parus cinereus*). The cinereus tit (of southern Asia) and Japanese tit (*P. minor*) (of East Asia) have been separated into two distinct species from the great tit (*P. major*) (Zheng 2023). In addition, snakes from Viperidae, Elapidae, and Colubridae have been reported to perform hiss displays (Møller et al. 2021a) and have large species richness in Hainan tropical rainforest (Wang 2014). In the rainforest, some snakes, such as *Sinonatrix percarinata* from Colubridae, have been found to prey on little torrent frogs. It is possible that the little torrent frogs may perceive risks from hisses of those snakes and birds.

Two experiments were designed for the hypothesis. In the first experiment, we used sound playbacks to test how little torrent frogs responded to white noise, zitting cisticola song, and snake hisses. In the second experiment, we used the sound playbacks to test how the little torrent frogs responded to white noise, great tit hisses (snake-like calls with low similarity), and zitting cisticola hisses (snake-like calls with high similarity). Anurans may perform fleeing behaviors when exposed to acoustic signals advertising risk information (Toledo et al. 2015; Hopkins and Folt 2019; Feagles and Höbel 2022). We predicted that frogs would flee from sound sources or adjust calling behaviors (e.g., ceasing calling and reducing call rate) if these snake and bird hisses served as alarm signals.

Methods

Playback sound files

Four types of sound stimuli were used in the first playback experiment. The first type was white noise (as a control) which was generated using Adobe Audition 3.0 software (Adobe Systems Inc., San Jose, CA, U.S.A.). The second type was a song of zitting cisticola. White noise playbacks increase background noise levels of focal locations, which may affect the behaviors of calling individuals. Zitting cisticola does not feed on frog species (Zhao 2001), and we selected it's song as an additional control. The third and fourth types were Gaboon vipers (*Bitis gabonica*) and king cobras (*Ophiophagus hannah*) hisses, respectively. Three types of sound stimuli were used in the second playback experiment. The first type was also white noise which was the same as the first experiment. The second and third types were snake-like hissing calls of great tits and zitting cisticolas, respectively. All hissing calls were obtained from a previous study (Barlow et al. 2023).

Hissing calls produced by zitting cisticola (Additional file 1) show the largest resemblance with snake hisses (Additional file 2 and 3) and appear in a same cluster with snake species in previous acoustic analysis (Barlow et al. 2023). Tits often utter sharp hissing calls (Additional file 4) that have similar acoustic spectral structure with snakes (Krams et al. 2014; Møller et al. 2021a), but the similarity is lower than zitting cisticola hisses. Great tit hisses show a percussive onset that is not found in zitting cisticola and snake hisses. As compared to great tits, the spectral traits of zitting cisticola hisses are more approximate to snake hisses (Fig. 1). For each song and snake-like hiss, two or three recording files from different individuals were chosen to make acoustic signals representative. The snake-like types are scarce and only two files were obtained for them. Snake hisses are also rare and only one recording was obtained for each species. Snake and snake-like bird hisses are poorly structured sounds and show little individual variation within species (Young et al. 1999; Dutour et al. 2020). So, the small size of such stimulus is also representative. All sound files were repeatedly copied and lengthened to 3 min. Then a 3 min quiet zone was inserted before and after the copied zone, respectively. Snake-like hisses from sympatric birds have long recordings and their natural repetitions were used during playbacks. Snake hiss recordings were short and their repetition rate (16 hisses per min) was set according to the average of sympatric bird hisses to make the stimuli similar to what the frogs would perceive in nature. All sound editing was conducted in Adobe Audition 3.0 software.

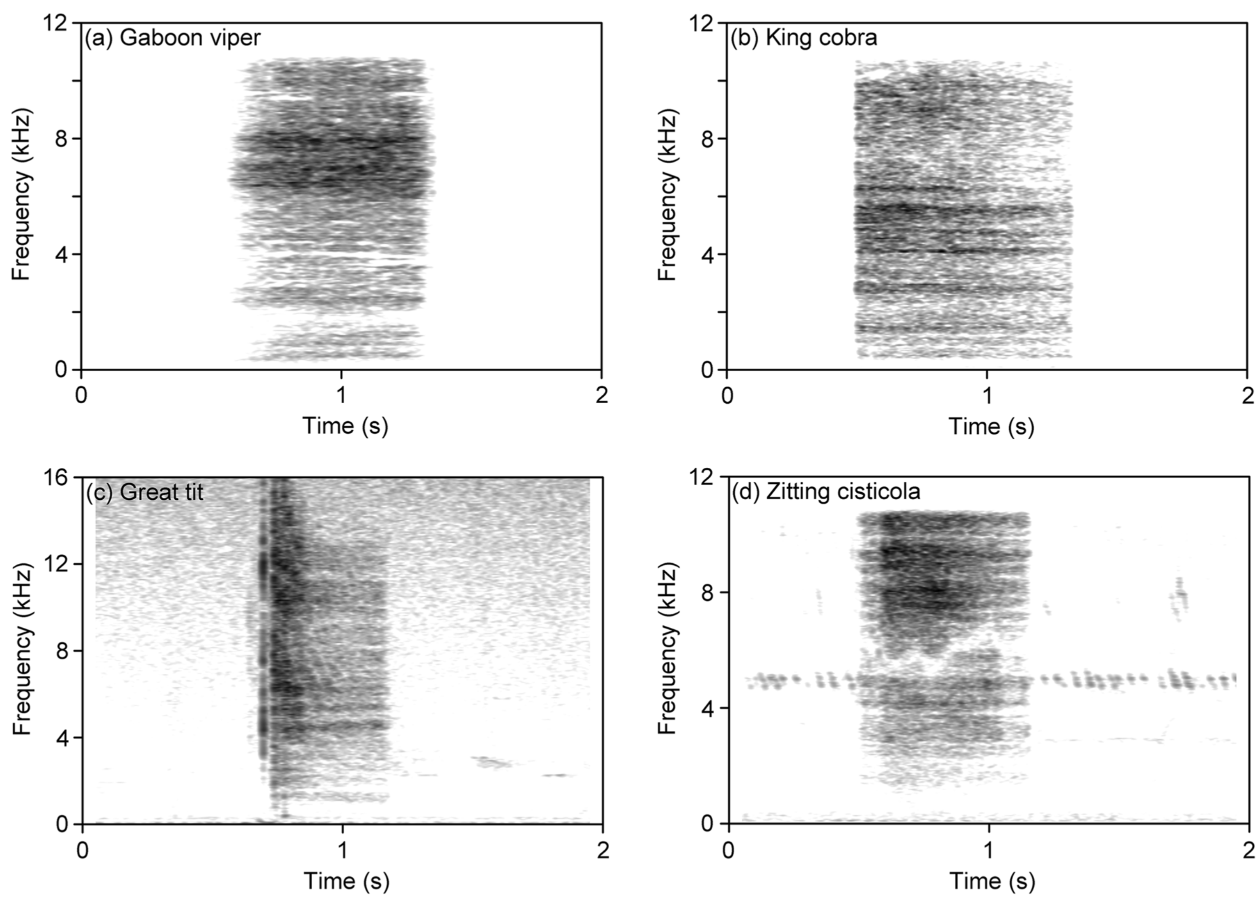

Fig. 1 Spectrogram comparisons of the Gaboon viper and king cobra hissing call (**a**, **b**), low snake-like hissing call of the great tit (**c**), and high snake-like hissing call of the zitting cisticola (**d**). As compared with great tit hiss, zitting cisticola hiss show a more similar frequency contour with snake hiss

Sound playback experiments

Sound playbacks were conducted in July 2022 (experiment 1) and June 2023 (experiment 2) at a tropical forest stream, Wuzhishan National Nature Reserve (109°32’-43’ E, 18°48’-59’ N), Hainan, south China. In playback experiments, a speaker (Clip3, JBL, USA) was fixed on a shelf bracket and placed at a 1 m distance to focal individual. When disturbed, little torrent frogs often move away from original position and jump into water. In this study, they were not observed to be disturbed by setting up the experiment. All stimuli were played via a digital voice recorder (ICD-PX470, Sony, Japan) connected to the speaker. During sound playbacks, the sound pressure levels (SPLs) of all stimuli were about 80 dB in the 1 m distance. Previous studies have shown that the amplitude approximates to the natural SPLs (75–85 dB) of avian hisses/calls (Møller et al. 2021a). In each experiment, different types of stimuli were stochastically broadcasted to avoid the effect of test sequence on behavioral response. One of two (or three) sound files was chosen when animals were presented with zitting cisticola songs, great tit hisses, and zitting cisticola hisses. The test processes and animals’ behavioral responses were recorded using a digital video camera (FDR-AX40, Sony, Japan). Next, we provided more details about the playback procedures.

Environmental fluctuation, such as diurnal temperature variation, may influence the ability of this species to perceive acoustic signals (Sun et al. 2020). To decrease the difference of weather condition, playback tests were only carried out between 8.00 and 14.00 on sunny days. The landscape is complex in Wuzhishan mountain streams in which high and precipitous places often have more background noise than other places. In order to increase signal-noise ratio (SNR), only frogs that called at relative flat terrains (low-noise locations) were considered as subjects. Three frogs were abandoned in the second experiment because they seldom called or stopped calling prior to the beginning of test. These rules allowed us to minimize environmental variation in different individuals. During breeding seasons, male little torrent frogs inhabit streams or nearby vegetation. Males are territorial and consecutively occupy a location for many days. Both experiments were completed within a few days, and males were tested in different locations (one frog was tested in a location). So, all individuals were not tested repeatedly in a same experiment.

Analysis and statistics

Three behaviors were analyzed by watching videos. Little torrent frogs prefer to call on the rocks in the stream. They would immediately jump into stream water when threatened. The number of escaping and not escaping individuals in each stimulus was calculated by observing whether animals jumped into the water. The number of calls in periods before, during and after each playback was determined by calculating the amount of vocal sac inflation. The number of ceasing/not ceasing calling individuals in different treatment groups was also calculated by watching the videos of all individuals. Males were considered as “individuals that ceased calling” if they stopped producing calls (call rate = 0) in the “during” period (i.e., 3 min stimulus presentation time). If not, they were considered as “individuals that continued to call” which may also reduce calling activity.

Fisher’s exact tests were employed to compare the number of escaping versus not escaping and calling versus not calling individuals in different playbacks. Binominal tests were used to analyze the probability of escaping and not escaping in different groups. A linear mixed model (LMM) with Gaussian distribution was used to evaluate the effect of sound playback on frogs’ calling activity. Prior to the test, the residuals of fitted values versus the residuals of variables were examined using a quantile-quantile plot to check the normality of all explanatory variables. In the model, individual number was considered as random effect and playback period was included as fixed factor. Weather conditions (sunny period, 22–25 ℃, ~ 90% relative humidity) in rainforest stream did not greatly fluctuate during the playbacks (between 8.00 and 14.00). Meanwhile, little torrent frogs are day-night calling species and remain a high calling activity during playback tests. Thus, the daily time was not included as a factor to avoid singular fitting. The calculation of degrees of freedom was based on Kenward-Roger method. For those significant dependent variables, post hoc pairwise tests were used to further compare the differences of calling activity in three periods (i.e., before, during and after playbacks). The LMM and post hoc pairwise tests were conducted utilizing the packages *lme4* (Bates et al. 2015) and *emmeans* (Fox and Weisberg 2011), respectively. All statistics were conducted in R v. 4.2.0 (R Core Team 2022).

Results

Experiment 1: snake hiss playbacks

To examine whether snake hiss can evoke anti-predator behavioral response, we tested a total of 20 calling individuals in the first experiment, which included four stimulus groups, that is, white noise (control 1), zitting cisticola song (control 2), Gaboon viper hiss, and king cobra hiss. A total of 20 trials were completed in each group. In this experiment, there was no difference in the number of escaping versus not escaping males across four treatment groups (0/20 vs. 0/20 vs. 1/19 vs. 0/20; Fisher’s exact test, $P = 1$).

Few individuals cease calling during white noise (0/20), zitting cisticola song (1/19), Gaboon viper hiss (1/19), and king cobra hiss (0/20) playbacks. The proportion of cease calling individuals showed no difference among four treatment groups (Fisher's exact test, $P=1$). Analyses on all individuals showed that little torrent frogs did not change their calling activity in response to playbacks of white noise (LMM, $\chi^2=1.14$, $df=2$, $P=0.567$; Fig. 2a), zitting cisticola song (LMM, $\chi^2=0.46$, $df=2$, $P=0.795$; Fig. 2b), and Gaboon viper hiss (LMM, $\chi^2=3.26$, $df=2$, $P=0.196$; Fig. 2c). However, their calling activity was significantly influenced by king cobra hiss (LMM, $\chi^2=7.31$, $df=2$, $P=0.026$; Fig. 2d). Post hoc pairwise tests showed that this species slightly decreased the number of calls during sound playbacks (before vs. during: 3.9 vs. 3.3 calls per 3-mins, $t=1.94$, $df=41.1$, $P=0.141$), but significantly increased this after the playbacks (during vs. after: 3.3 vs. 4.1 calls per 3-mins, $t=2.67$, $df=41.3$, $P=0.029$).

Experiment 2: avian hiss playbacks

To examine whether snake-like bird hiss can evoke anti-predator behavioral response, we tested a total of 16 calling individuals in the second experiment in which 13, 15, and 15 trials were completed in white noise, great tit hiss, and zitting cisticola hiss playbacks, respectively. In the second experiment, there was no difference in the number of escaping versus not escaping individuals among three treatment groups (1/12 vs. 0/15 vs. 1/14; Fisher's exact test, $P=0.751$).

No individual stopped calling when frogs were presented with white noise (0/13) and great tit hiss (0/15), while 1/3 individuals (5/15) ceased calling in response to zitting cisticola hiss. Three treatment groups had a significant difference in the probability of stop calling (Fisher's exact test, $P=0.008$). White noise (LMM, $\chi^2=5.29$, $df=2$, $P=0.071$; Fig. 3a) and great tit hiss (LMM, $\chi^2=2.84$, $df=2$, $P=0.242$; Fig. 3b) had no significant effect on calling activity of little torrent frogs. Zitting cisticola hiss,

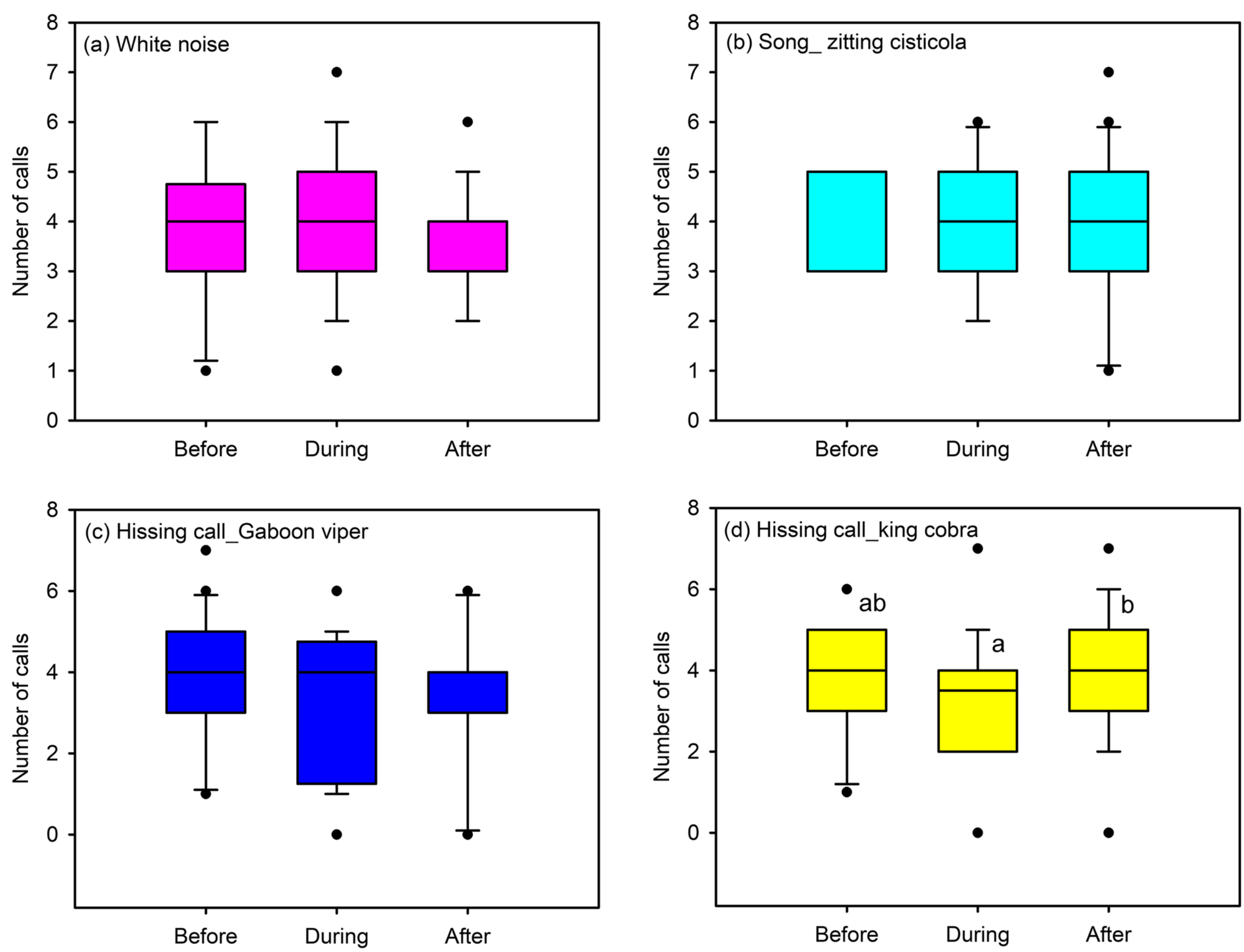

Fig. 2 Differences of calling activity in three periods (i.e., before, during and after) of white noise (**a**), zitting cisticola song (**b**), Gaboon viper hiss (**c**), and king cobra hiss playbacks. Different letters indicate $P< 0.05$

however, showed a significant effect on the calling activity (LMM, $\chi^2=8.44$, $df=2$, $P=0.015$; Fig. 3c). Further pairwise analyses suggested that little torrent frogs significantly decreased the number of calls during zitting cisticola hiss playbacks (before vs. during: $t=3.011$, $df=32.1$, $P=0.014$; Fig. 3c).

Discussion

We found that little torrent frogs did not escape in response to sound playbacks of white noise, snake hisses, and snake-like avian hisses. However, they significantly changed calling activity during sympatric snake hiss playbacks. Moreover, snake-like avian hiss evoked a significant decrease in the calling activity of the little torrent frog. These results show that sympatric snake and avian hisses can be recognized as alarm signals by frogs and evoke their anti-predator responses.

Visually dependent predators (e.g., some birds) often search for frog prey according to their movements (Paluh et al. 2014), while sound dependent predators/parasites (e.g., some bats and insects) usually locate frogs by their acoustic displays (Bernal et al. 2006; Meuche et al. 2016; Zhao et al. 2022b). Avian hiss is a specific vocal mimicry on snake species (Rowe et al. 1986; Møller et al. 2021a, b), which may transmit risk information to frogs due to the predator-prey relationship between snakes and anurans. For little torrent frogs, acoustic signals (or vocal-sac movements) are prone to expose the location of calling individuals to potential parasites (Zhao et al. 2022b) or predators (e.g., birds). Thus, they are expected to reduce calling behaviors when exposed to risk messages. Similar to zitting cisticola hiss, cobra hiss also decreased the calling activity (before vs. during: 3.9 vs. 3.3 calls per 3-min recording), but the difference between "before" and "during" was not significant. However, there was a significant increase after the playbacks (during vs. after: 3.3 vs. 4.1 calls per 3-min recording). In this study, snake hiss playbacks were conducted in June 2023 during which background noise in streams was louder than July 2022 when bird hiss playbacks were conducted. The noise difference between two periods was mainly caused by local rainfall variation. Some studies suggest noise affects animals' ability to assess risks and change their behavioral responses (e.g., Chan et al. 2010). In noisier streams, it is more challenging to detect and recognize hissing calls. It is possible that louder habitat noise decreases signal-noise ratio and makes acoustic detection and recognition more difficult, which may cause the behavioral difference between zitting cisticola and cobra hiss playbacks.

The structured vocal signals often show some individual variation in many species. Therefore, multiple or representative calls are often used in playback tests to avoid potential biases. In this study, however, we only had one or two hissing stimulus from each species due to the difficulties in obtaining more recordings. Snake and bird hisses are poorly structured signals and are often described as "nothing more than loud" (Young et al. 1999; Møller et al. 2021a). In other words, these hisses do not have so much individual variation as most vocal signals. We thus argue that the results of this study may not be biased by the small size of stimulus. However, further studies with more stimulus samples and species are still needed to provide more compelling evidence.

Both conspecific and heterospecific acoustic eavesdropping are revealed in anuran species. They may discriminate dangerous information from alarm calls and perform different response strategies. For instance, smoky jungle frogs (*Leptodactylus savagei*) flee into hidden places when presented with conspecific calls advertising predation events (Hopkins and Folt 2019). Some anurans, however, did not escape or hide in response to conspecific alarm or distress calls (Dapper et al. 2011; Forti et al. 2017). Instead, they just cease or decrease calling behaviors. Studies of two neotropical treefrogs show that males quickly stop calling or reduce their call rate after hearing conspecific distress calls (Forti et al. 2017). In túngara frogs (*Engystomops pustulosus*), chorus cessation is initiated by sudden silence of a few

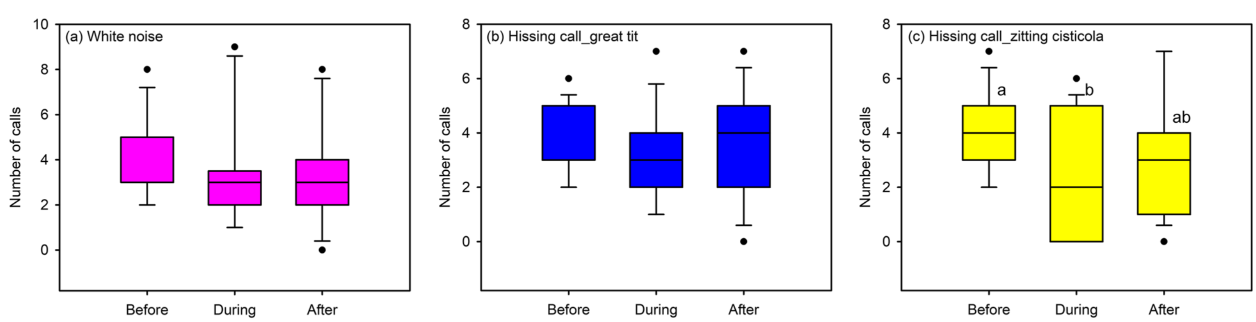

Fig. 3 Differences of calling activity in three periods (i.e., before, during and after) of white noise (**a**), great tit hiss (**b**), and zitting cisticola hiss (**c**) playbacks. Individuals that cease calling are also included in the analysis. Different letters indicate $P < 0.05$

calling individuals, which may be due to the relevance with a predator (Dapper et al. 2011). Moreover, this species called more in response to sympatric heterospecific alarm calls (Phelps et al. 2007). Torrent frogs have similar body color with environmental background (Zhao et al. 2021). It's less likely to be detected if they decrease or interrupt calling and inhabit a site where background color is similar with body color (Zhao et al. 2018). In addition, snakes do not hiss when they hunt prey (Møller et al. 2021a). In other words, the hiss sound is not emitted during the hunting sequence. So it may serve as social or public information and be used to by frogs to defend themselves from predators. Rather than a cue used to locate a threat from the snake.

Snake-like hisses of avian species may advertise both bird and snake enemies to frog species. Great tit and zitting cisticola are small birds and primarily feed on plant foods, insects as well as other small invertebrates (Zhao 2001). In other words, anurans are not their prey. Therefore, snake-like hissing calls of great tit and zitting cisticola might not advertise avian predators to anuran species. This is further demonstrated by zitting cisticola song playbacks and a previous study on great tit (Zhao et al. 2022a). A highly snake-like hiss may deceive avian predators and thus be useful for bird prey. In this study, we show that zitting cisticola hisses induce a similar anti-predator response with snake hiss.

Snake hisses have a high degree of similarity across species, which may provide warning signals for frogs. However, we found a different response in an allopatric snake hiss produced by Gaboon viper. In this study, king cobra (sympatric) and Gaboon viper (allopatric) hisses have different frequency distributions (Fig. 1). Such variation may be related to their different responses. Moreover, calling loudness also affects the propagation distance of acoustic signals (Nemeth and Brumm 2010). Apart from calling activity and motion, little torrent frogs may also adjust their acoustic loudness in response to hiss playbacks, which needs further study in the future.

Visual mimicry has been investigated in many species, while acoustic mimicry receives less attention (Dutour et al. 2020). Several avian species have been shown to mimic snake hisses and use snake-like hisses to deter competitors and increase survival chances (Dutour et al. 2020; Møller et al. 2021b). In this study, we show that a snake-like hiss produced by zitting cisticola can be recognized as a risk signal and induce a similar anti-predator response with sympatric snake hiss in a torrent frog. This study increases evidence for anuran heterospecific eavesdropping on predator calls. Such ability is less demonstrated in amphibians. Therefore, this study increases our understanding of the evolution of predator recognition in vertebrates. However, it remains unclear how the perception and recognition are achieved and whether other anurans respond similarly to such stimulus.

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Authors' contributions
WL, LZ and JW conceived the study; LZ, YQ and YJ performed the experiments; LZ analyzed the data and wrote the draft manuscript. LZ prepared figures 1-3. WL and JW revised the manuscript. All authors reviewed and approved the final manuscript.

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Availability of data and materials
No datasets were generated or analysed during the current study.

Declarations

Ethics approval and consent to participate
No research permit was required for this study. The experiments comply with the current laws of China. All procedures were approved by the Animal Research Ethics Committee of Hainan Provincial Education Centre for Ecology and Environment, Hainan Normal University (permit no. HNECEE-2020-005).

Competing interests
The authors declare no competing interests.

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