

Article

# Parent–offspring and inter-offspring responses to conspecific versus heterospecific distress calls in 2 sympatric birds

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Handling editor: Zhi-Yun Jia

Received on 16 October 2021; accepted on 21 December 2021

## Abstract

Distress calls, as a type of alarm call, play important roles in expressing bodily condition and conveying information concerning predation threats. In this study, we examined the communication via distress calls in parent–offspring and inter-offspring interactions. First, we used playback of chick distress calls of 2 sympatric breeders, the vinous-throated parrotbill *Sinosuthora webbiana* and the oriental reed warbler *Acrocephalus orientalis*, to the adults/chicks of these 2 species, respectively, and measured the responses of conspecifics or heterospecifics. The playback-to-chicks experiment showed that both species of chicks reduced the number of begging calls and begging duration time as a response to conspecific/heterospecific distress calls compared with natural begging and background noise controls. However, reed warbler chicks also reduced beak opening frequency in the response to conspecific distress calls compared with other playback stimuli. Second, the results of the playback-to-adults experiment showed that reed warbler adults could eavesdrop on distress calls of conspecific neighbors and sympatric heterospecifics. Furthermore, the nest-leaving behavior of reed warblers did not differ significantly when they heard the distress calls of conspecifics or parrotbills. Finally, reed warbler adults responded to heterospecific distress calls more quickly than to conspecific distress calls, and parrotbill adults presented the same response. Our results supported the warn-kin hypothesis and show that chick distress calls play an important role in conveying risk and the condition of chicks to enhance individual fitness. In addition, we also found that eavesdropping on distress calls is a congenital behavior that begins in the chick stage.

**Key words:** acoustic communication, call recognition, chick–chick system, eavesdropping, parent–offspring system.

Public information (PI) is a form of indirect social information that can be acquired in various ways by noting the performance and the behavioral decisions of other individuals. Species can eavesdrop on PI to reduce uncertainty concerning the environment (Valone 2007). Prey that shared predators could recognize and respond to vocal information of other species; this would increase the perception of risk in the habitat. Among vocal signals, distress calls are a common form of communication in the animal kingdom. Many species of

mammals (Fenton et al. 1976; Rendall et al. 2009; Froidevaux et al. 2020; Hörmann et al. 2021), birds (Brémond and Aubin 1990; Conover 1994; Benedict 2007), reptiles (Roberto and Botero-Arias 2013; Ruiz-Monachesi and Labra 2020), and amphibians (De Toledo et al. 2009) emit distress calls. Distress calls are a type of alarm call related to anti-predator defense or calling for help (Magrath et al. 2015). Both infants and adults can emit these signals to express their body condition (Lingle et al. 2012; Carter et al. 2015). Meanwhile,

viral infections may alter distress calls used in an anti-predator context within birds, thus potentially reducing fitness both directly (through disease) and indirectly (through increased predation; Laiolo et al. 2007). These calls are complex, showing a wide frequency range and harmonic structure and being generally modulated via frequency (Venuto et al. 2001). Distress calls can evoke interspecific responses that are associated with similarities in acoustic structure (Aubin 1991). Because distress calls are reliable signals of predation risk, individuals recognizing the calls and responding correctly would increase the probability of survival for both conspecifics and heterospecifics (Högstedt 1983; Caro 2005). Eavesdropping is a widespread behavior that functions to update estimates of the quality of other individuals (Valone 2007). The basis of recognition of heterospecific and conspecific distress calls may include 3 aspects: learning, similarity in acoustic parameters, and phylogenetic relatedness (Wu et al. 2021). Therefore, whatever distress calls chicks or adults utter, this information would be valuable for sympatric neighbors. Distress calls may also convey information about the quality of the prey to predators (Laiolo et al. 2004).

There are several mutually nonexclusive hypotheses that have been proposed to explain why birds emit distress calls: (1) the caller requests aid from kin or unrelated reciprocators (the request-aid hypothesis; Rohwer et al. 1976); (2) the caller warns kin about the predator as an altruistic act that enhances relatives' fitness (the warn-kin hypothesis; Rohwer et al. 1976); (3) the caller startles the predator to effect release (the startle-predator hypothesis; Driver and Humphries 1969); (4) the caller attracts other predators to distract the first predator and facilitate prey escape (the predator-attraction hypothesis) (Curio 1976); and (5) the caller attracts an audience to learn about predators from watching predator-prey interactions (the attract-audience hypothesis; Conover 1987). There may be multiple functions for distress calls, and thus, observations supporting one hypothesis do not disprove another. For example, birds may produce distress calls to simultaneously request aid and startle the predator (Wise et al. 1999).

In birds, distress calls play an important role in parent-offspring interactions. Chicks' distress calls express stressful conditions or the presence of danger (Bermant 1963), although parents can respond to a chick's distress calls to reduce the danger, for example from a predator (Loth et al. 2018). These interactions may ensure parental reproductive success and thereby enhance individual fitness. In contrast, failure to respond may result in the death of signaling offspring or siblings (Benedict 2007). For example, greylag geese *Anser anser* pairs perceived goslings' distress calls as stressful and alerting and responded with increased comforting and vigilance behaviors (Loth et al. 2018). Meanwhile, distress calls may also contribute to sibling communication. For precocial birds, chicks easily become lost, and young birds tend to produce distress calls that are assumed to help re-establish contact with a parent (Lamprecht 1985). Similarly, for altricial birds, chicks cannot escape as quickly as adults; consequently, they may stay still or keep silent to avoid predators detecting the cues signaling the existence of a prey item after hearing parents' or other species' alarm calls (Madden et al. 2005; Haff and Magrath 2012). Therefore, distress calls may include risk information in both precocial and altricial birds. However, despite its importance in sibling and parent-offspring communication, we still have little knowledge concerning the recognition mechanism of distress call communication (Magrath et al. 2015).

To the best of our knowledge, most previous research has focused on studying distress calls in adults (Koenig et al. 1991;

Conover 1994; Wise et al. 1999), while the chick stage has received much less attention. Here, we study adult-offspring and inter-offspring conspecific communication and eavesdropping via chick distress calls in the vinous-throated parrotbill (VP) *Sinosuthora webbiana* and oriental reed warbler (ORW) *Acrocephalus orientalis*. These 2 species have sympatric breeding habitats, large populations, and share the same predators. However, their chicks produce significantly different distress calls (see Materials and Methods for details). Therefore, the species provide an opportunity to test the recognition of conspecific/heterospecific chicks' distress calls. We recorded the chick distress calls of these 2 species, analyzed their differences, and used playback to conspecific and heterospecific adults/chicks. The aim of this study was to test whether VP/ORW adults and offspring would be able to recognize and respond to conspecific/heterospecific distress calls of chicks. First, because distress calls involve threatening information, we predicted that compared with unthreatening controls (natural begging), both the VP and ORW chicks would suppress their begging behavior as a response to the conspecific distress calls. Second, we predicted that the adults of these 2 species of birds would respond to the distress calls by leaving their nests. Third, we predicted that the VP/ORW chicks would also suppress their begging behavior toward heterospecific distress calls (to some extent), because sympatric species may be able to eavesdrop on threatening information. For the same reason, we also predicted that the VP/ORW adults would respond to heterospecific distress calls (to some extent) by leaving their nests compared with unthreatening control stimuli.

## Materials and Methods

### Study area

The study was carried out in the Yongnianwa National Natural Park, Yongnian district, Hebei province (36°40'60"–36°41'06"N, 114°41'15"–114°45'00"E). The park is located in a lowland wetland in China, and the wetland is only 40.3 m above sea level. The average rainfall is 527.8 mm, and the average annual temperature is 12.9°C. The main vegetation in this area includes reeds *Phragmites australis*, cattails *Typha latifolia*, and other herbaceous species (Wang and Yang 2020). There are many species of predators for VP and ORW in this wetland, including the Siberian weasel *Mustela sibirica*, the Erythema snake *Dimodon rufozonatum*, and the Brown rat *Rattus norvegicus*. We conducted the playback experiments in thickets and reeds where VPs and ORWs are found.

### Subjects

Large populations of VP and ORW exist in sympatry in the wetland. The breeding nests of VP and ORW were distributed in a mosaic pattern within the habitat, with similar nest structures and nest sites in this wetland (Ma et al. 2021). The chicks of ORW are larger than those of VP. For VP and ORW, the growth curves of weight and length of nestlings corresponded to Logistic curves. The chicks of the 2 species have similar fledging periods (12–13 days; Guo et al. 2006; Wang et al. 2013).

### Production of playback sounds

By monitoring the nests of these 2 species, we chose 8-day-old chicks for distress call recording, because according to our observations such chicks are old enough to react to threats (i.e., human capture in this case) by producing distress calls. We prompted the chicks from different nests (one chick from each nest) to produce distress calls by

**Table 1** Comparison of 5 acoustic parameters of BSs of chick distress calls between the VP and the ORW in Yongnianwa National Natural Park (Mann–Whitney *U* test; Student's *t*-test) AQ

Parameter of phrase	VP ( <i>n</i> = 13)	ORW ( <i>n</i> = 13)	<i>w</i>	<i>P</i> -value
Lowest frequency/kHz	1200.63 ± 15.42	668.59 ± 6.2	155	< 0.001
Peak frequency/kHz	2260.26 ± 18.59	1648.22 ± 11.85	151	< 0.001
	VP ( <i>n</i> = 13)	ORW ( <i>n</i> = 13)	<i>t</i>	<i>P</i> -value
Duration/s	0.37 ± 0.002	0.3 ± 0.002	2.4	0.02
Highest frequency/kHz	2561 ± 19.44	2208.4 ± 10.18	2.66	0.02
Delta frequency/kHz	1361.1 ± 8.08	1543.28 ± 9.52	-2.79	0.01

removing them from the nests and then recorded 1–2 min of distress calls in WAV format (*n* = 13 for chicks of VP and ORW) by using an audio recorder (Sony PCM-A10, Tokyo, Japan). Chicks were put back to the nest after we recorded the distress calls, and all were accepted by their parents. The sampling frequency was 44.1 kHz, and the sampling resolution was 16 bits. We analyzed 5 acoustic parameters of basic sound (BS) using Raven Pro version 1.4 in each phrase of distress calls: (1) duration; (2) lowest frequency; (3) highest frequency; (4) delta frequency; and (5) peak frequency. According to whether the data followed a normal distribution, we conducted Mann–Whitney *U* tests or Student's *t*-tests. According to the results of comparisons between these 2 species, significant differences were detected in all 5 parameters [number of calls: 1408 (VP); 988 (ORW); Table 1].

To avoid pseudo-replication in playback experiments, we randomly chose 3 chicks from each species and combined their distress calls as playback sounds. The chicks that were used to record the distress calls were excluded from the playback experiment. To obtain high-quality distress calls, we used Raven Pro version 1.4 software (Cornell lab of ornithology, Cornell University) to chip the sound that we recorded, removed noise below 0.2 kHz, and randomly combined the recordings to form 30 and 60 s distress calls (Wang and Yang 2020), but we did not change the syllable type or call rate in the segment of distress calls. We recorded the background noise from the wetland and randomly chose and chipped the background noise to make 3 0.3-s sound fragments, and we randomly combined these fragments to form the 30 and 60 s background noise (Supplementary Figure S1).

The playback experiments included 2 parts, the playback to chicks and the playback to adults (clarified in the section below). For the playback-to-chicks experiment, the playback stimuli consisted of 3 sets of independent sounds: 30 s of VP distress calls, ORW distress calls, and background noise. Each set of sounds was played at the same distance of 1 m and the same sound pressure level (SPL) of 60 dB. This SPL standard was based on our SPL measurements of chick distress calls at 1 m distance using a sound meter (Smart Sensor, AR824, Dongguan, China). The amplitude was close to the natural level when we recorded the distress calls [VP: 57.79 ± 0.84 dB (mean ± Standard Error); ORW: 62.63 ± 1.40 dB (mean ± SE)]. The playback stimuli for the playback-to-adults experiments were the same, except that the duration of each set of sounds was 60 s. The playback time to chicks was shorter than to adults, because we considered that chicks were too fragile to endure a longer time.

### Playback experiments

We chose 5-day-old old chicks for the playback-to-chicks experiment, because in this stage, they start to produce obvious begging

calls. Moreover, the chicks' eyes are barely open; so, they were not alarmed by humans. We randomly removed 1 chick from each nest (*n* = 15 for VP and *n* = 11 for ORW) to the indoor lab of the study area in order to avoid any interference such as reactions from nest-mates and parents. The chicks were weighed with an electronic scale (Yuedi Electronic scale, Shenzhen, China), placed into an empty nest that was collected during the previous year, and then left alone for 40 min before the initiation of the experiment to make the chicks hungry. A digital video camera (Sony HDR-PJ510E, Tokyo, Japan) and a sound recorder (Sony PCM-A10, Tokyo, Japan) were mounted nearby to record the begging behaviors of chicks, although a Bluetooth speaker (ShiDu P3, Shenzhen, China) was placed at a distance of 1 m from the chicks for playback of distress calls. During the experiment, an observer (Y.J.) simulated parent visitation by lightly touching the edge of the nest (one touch/3 s) to stimulate begging behavior of the chicks. The playback experiment was composed of 30 s of behavior and acoustic recording without playback (natural begging) following the playback stimuli (i.e., playing 30 s of VP distress calls, ORW distress calls, and background noise in random order). Therefore, the playback experiment included 4 trials (30 s for each trial), and the interval between trials was 5 min for return to the base conditions. We conducted playback with the video and sound recording to quantify 3 aspects of begging behavior: (1) number of beak openings; (2) the number of begging calls; and (3) begging duration (time of beak opening) during each 30 s of observation. Each chick was returned to its own nest after the 1 h experiment. All chicks were accepted by their own parents and were given food by their parents as normal.

The playback-to-adults experiment was conducted during the early egg incubation stage [days after clutch completion (mean ± SE), VP: 2.14 ± 0.23, *n* = 14; ORW: 2.22 ± 0.19, *n* = 18] rather than in the chick stage to avoid interference of begging from chicks. A micro camera (WJO3, Hisilicon, Shenzhen, China) was mounted 30 cm above the observed nest to record the parent birds' behavior, although a Bluetooth speaker (ShiDu P3, Shenzhen, China) was placed at a distance of 1 m and at the same height as the nest for playing distress calls. The playback was initiated 2 min after the parents returned to the nest for incubation. The playback stimuli were the same as in the playback-to-chick experiment, except that each set of sounds was 60 s in duration, and the interval between playbacks was 30 min. The playback order was also random, and the neighboring nest would not be sampled for the playback experiment. Two aspects of parental reactions were recorded: (1) nest-leaving behavior: whether parents left the nest (yes/no) after the playback and (2) leaving time: when the parents left the nest (0–61 s) during playback. If the parents left the nest during playback, the time of leaving ranged from 0 to 60 s. If the parents did

not leave the nest during playback, the leaving time was set to 61 s based on a standard method of adding 1 U to the maximum value (Wu et al. 2021).

**Statistical analyses**

For all playback experiments, we tested the carryover effect produced by the order of presentation due to the recovery time between stimuli. The order of presentation was used as an independent variable in all trials using generalized linear mixed-effect models (GLMMs). The results showed that there was no carryover effect of order presentation in all trials ( $P > 0.05$ ).

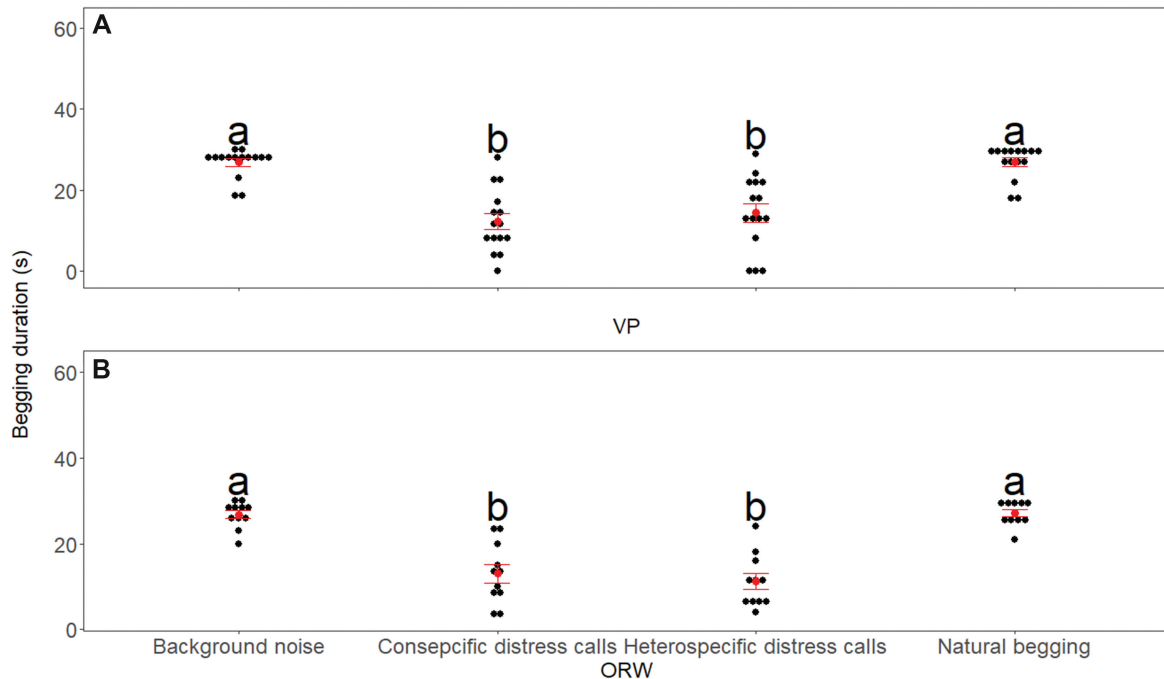
For the playback-to-chicks experiment, GLMMs with Poisson distribution were used in each dependent variable, in which the response variable was the beak opening frequency, the number of begging calls, or begging duration, while the playback treatment had 4 levels (natural begging, VP and OWR distress calls, and background noise). The individual identity was included as a random-effect factor, and body weight was included as a covariate. Then, chi-square tests were used to obtain  $P$ -values by comparing the fitted models to null models of random effect. In addition, we also used marginal pseudo- $R^2$  to evaluate the effect size of fixed-effect factors via the R package MuMIN (Nakagawa and Schielzeth, 2013).

For the playback-to-adults experiment, GLMMs with binomial distributions were used to test differences in parental behavior (the response variable being left/did not leave the nest during playback) among 3 playback stimuli. We also used GLMMs with a Poisson distribution to analyze the leaving time. Nest identity, egg-laying day, and clutch size were included as random-effect factors. We used chi-square tests to obtain  $P$ -values by comparing the fitted model to a null model of random effect. Finally, we used marginal pseudo- $R^2$  to evaluate the effect sizes of fixed-effect factors. All GLMMs were evaluated using the lme4 package within R version 4.0.5.

**Results**

In the playback-to-chicks experiment, the begging duration of both VP and ORW chicks differed among the playback stimuli (VP:  $\chi^2 = 144.68$ ,  $P < 0.001$ , marginal pseudo- $R^2 = 0.57$ ; ORW:  $\chi^2 = 132.16$ ,  $P < 0.001$ , marginal pseudo- $R^2 = 0.73$ , GLMMs; Figure 1). Both the conspecific and heterospecific distress calls reduced the begging duration in the chicks of these 2 bird species compared with natural begging and background noise control, but no difference was found in the begging duration after conspecific or heterospecific distress calls for both species (Figure 1 and Table 2). The number of begging calls also differed among the playback stimuli (VP:  $\chi^2 = 200.88$ ,  $P < 0.001$ , marginal pseudo- $R^2 = 0.63$ ; ORW:  $\chi^2 = 156.06$ ,  $P < 0.001$ , marginal pseudo- $R^2 = 0.80$ , GLMMs; Figure 2). Both species of chicks reduced the number of begging calls after hearing conspecific/heterospecific distress calls compared with natural begging and background noise, but there was no difference between the number of begging calls to conspecific or heterospecific distress calls for both species (Figure 2). For the VP, there was no difference in the number of beak openings among the playback stimuli ( $\chi^2 = 3.20$ ,  $P = 0.52$ , marginal pseudo- $R^2 = 0.05$ , GLMMs; Figure 3). However, for the ORW chicks, the conspecific distress calls reduced the beak opening frequency compared with the heterospecific distress calls, natural begging, and background noise ( $\chi^2 = 9.48$ ,  $P = 0.04$ , marginal pseudo- $R^2 = 0.20$ , GLMMs; Figure 3; and Table 2). We found that body weight had no effect on the 3 response variables of VP ( $P > 0.05$ ) and also had no effect on the number of begging calls or beak opening frequency of ORW ( $P > 0.05$ ). However, body weight had a significant effect on begging duration of ORW ( $P = 0.02$ ).

In the playback-to-adults experiment, the female ORW left their nests more frequently following conspecific/heterospecific distress calls compared with background noise ( $\chi^2 = 24.79$ ,  $P < 0.001$ ,

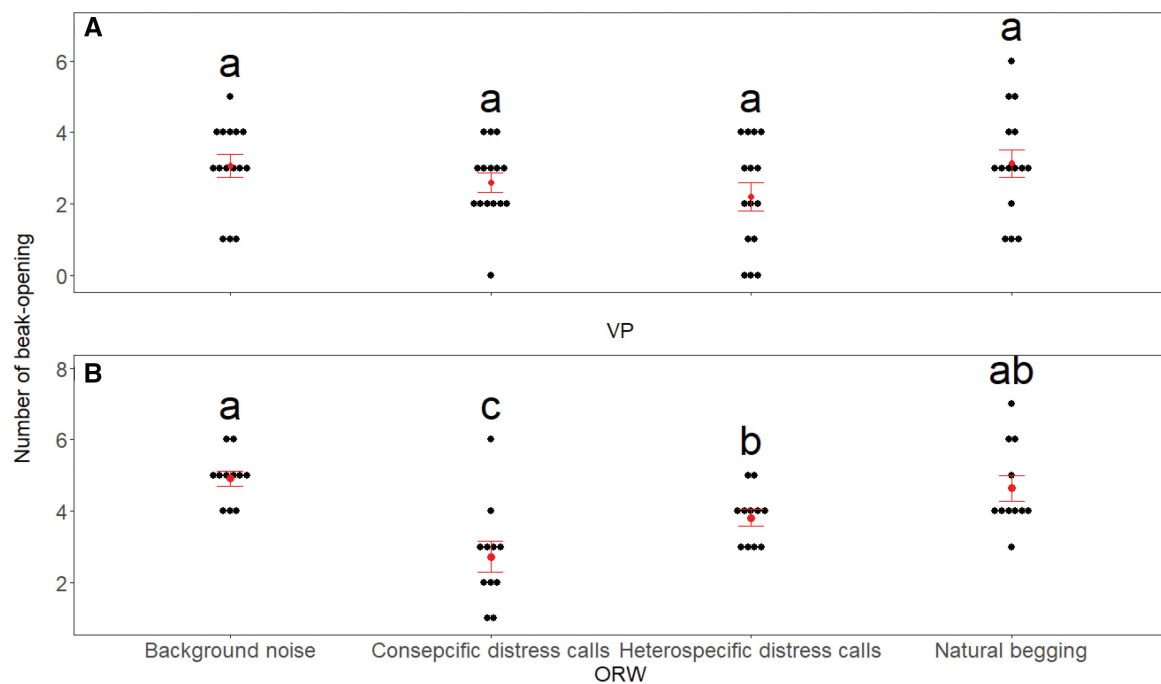


**Figure 1.** Comparison of begging duration from nests as a response to playback stimuli between (A) the VP and (B) the ORW in the playback-to-adults experiment. The red points and whiskers represent mean and standard errors of the observed data, respectively. The black points represent the raw data, whilst treatments with same/different letters indicate nonsignificant ( $P \geq 0.05$ )/significant ( $P < 0.05$ ) differences in responses, respectively.

**Table 2** A summary of the results of 3 GLMMs for the responses of begging duration, number of begging calls, or beak opening frequency to different treatments by VP and ORW chicks in the playback-to-chicks experiment

Response variable	Natural begging as the baseline level (VP)			Response variable	Natural begging as the baseline level (ORW)		
	SE	Z	P-value		SE	Z	P-value
Begging duration, marginal pseudo- $R^2 = 0.57$ (VP) and 0.73 (ORW)							
Intercept	0.52	7.46	< 0.001	Intercept	0.28	10.16	< 0.001
Conspecific distress calls	0.09	-8.86	< 0.001	Conspecific distress calls	0.10	-7.23	< 0.001
Background noise	0.07	0.035	0.97	Background noise	0.08	-0.12	0.9
Heterospecific distress calls	0.08	-7.49	< 0.001	Heterospecific distress calls	0.11	-8.26	< 0.001
Number of begging calls, marginal pseudo- $R^2 = 0.63$ (VP) and 0.8 (ORW)							
Intercept	0.69	5.12	< 0.001	Intercept	0.09	29.26	< 0.001
Conspecific distress calls	0.11	-9.3	< 0.001	Conspecific distress calls	0.16	-7.76	< 0.001
Background noise	0.08	0.12	0.9	Background noise	0.11	-0.27	0.79
Heterospecific distress calls	0.11	-9.4	< 0.001	Heterospecific distress calls	0.17	-8.20	< 0.001
Beak opening frequency, marginal pseudo- $R^2 = 0.05$ (VP) and 0.2 (ORW)							
Intercept	0.62	1.97	0.05	Intercept	0.44	4.50	< 0.001
Conspecific distress calls	0.22	-0.86	0.39	Conspecific distress calls	0.05	-1.09	0.02
Background noise	0.21	-0.1	0.92	Background noise	0.20	0.29	0.77
Heterospecific distress calls	0.23	-1.56	0.12	Heterospecific distress calls	0.21	-0.93	0.07

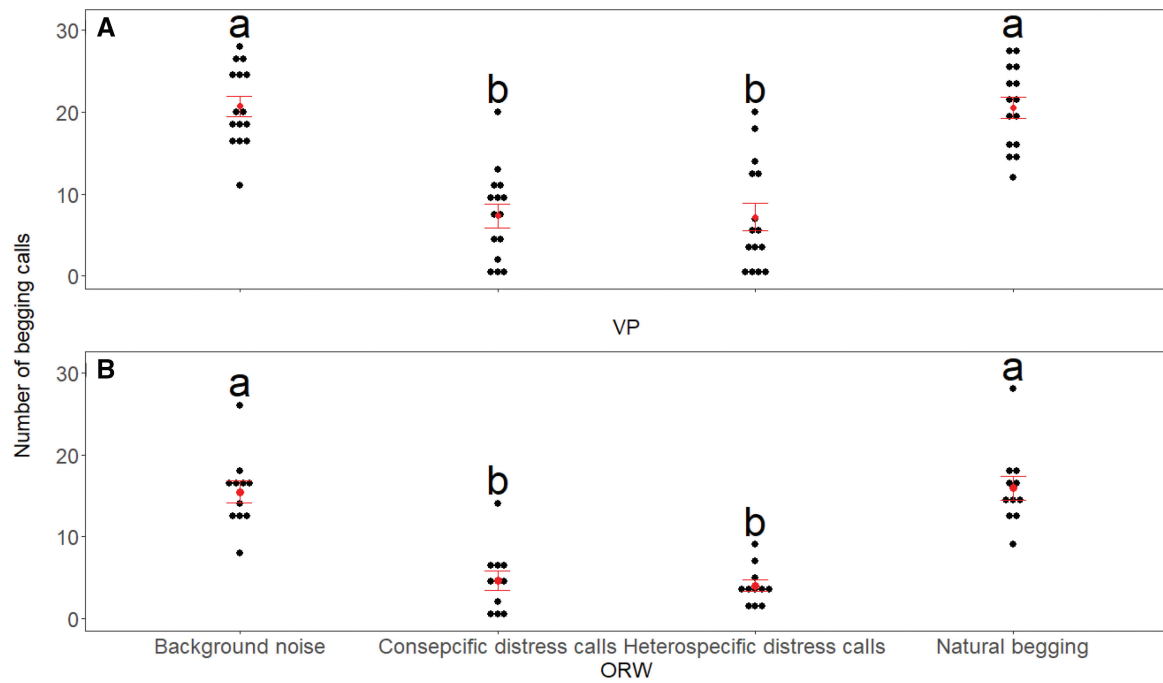
P-values (for model variables) <0.05 are highlighted in bold. Pseudo- $R^2$  for each model is shown to quantify the effect sizes for stimuli as predictor variables.

**Figure 2.** Comparison of the number of begging calls from nests as a response toward playback stimuli between (A) VPs and (B) ORWs in the playback-to-adults experiment. The red points and whiskers represent mean and standard errors of the observed data, respectively. The black points represent the raw data, while treatments with same/different letters indicate nonsignificant ( $P \geq 0.05$ )/significant ( $P < 0.05$ ) differences in responses, respectively.

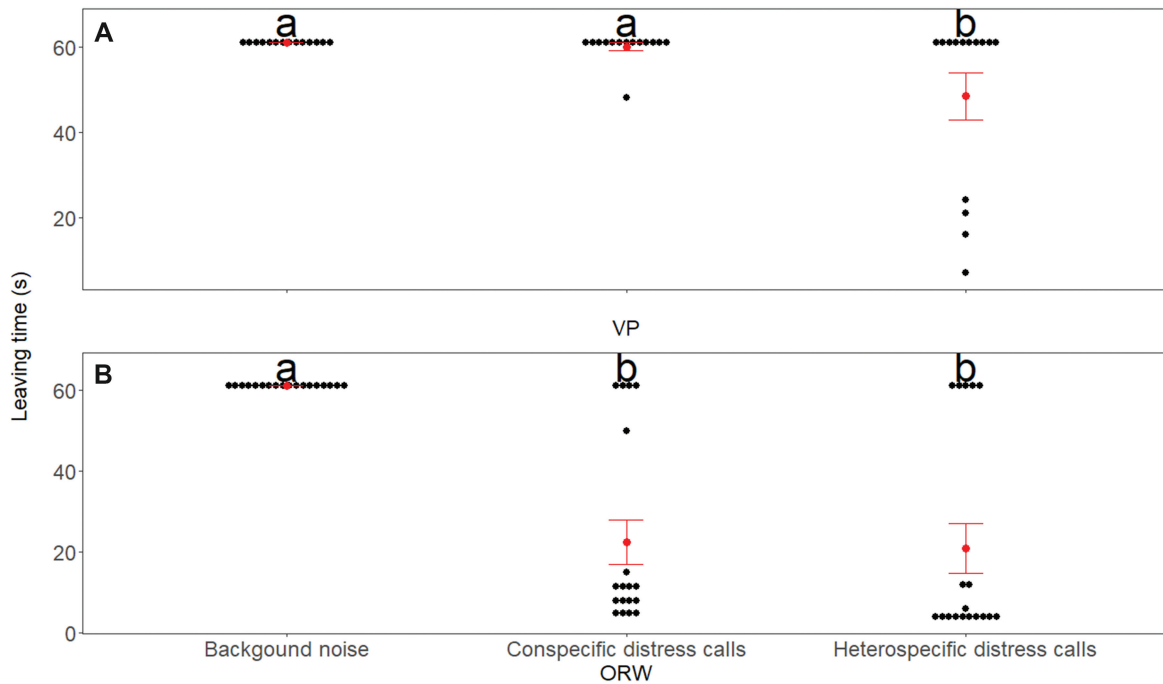
marginal pseudo- $R^2 = 0.47$ , GLMMs), and no difference was found between their responses to conspecific and heterospecific distress calls. The number of ORW individuals that left their nests according to conspecific distress calls, heterospecific distress calls, or background noise ( $n = 18$  for each trial) was 12, 14, and 0, respectively. However, this variable did not differ among playback stimuli for VP ( $\chi^2 = 2.37$ ,  $P = 0.12$ , marginal pseudo- $R^2 = 0.04$ , GLMMs). The corresponding values for conspecific distress calls, heterospecific distress calls, and background noise

( $n = 14$  for each trial) were 4, 1, and 0, respectively. It appeared that VP parents (4, 1, and 0) were less willing to leave their nests than ORW (12, 14, and 0).

The second response variable (i.e., leaving time) differed among playback stimuli for VP ( $\chi^2 = 19.60$ ,  $P < 0.001$ , marginal pseudo- $R^2 = 0.22$ , GLMMs, Figure 4A). VP adults left their nests faster after heterospecific distress calls (mean  $\pm$  SE = 48.43  $\pm$  5.60), followed by conspecific distress calls (mean  $\pm$  SE = 60.07  $\pm$  0.93), and finally the background noise (mean  $\pm$  SE = 61  $\pm$  0). For ORW,



**Figure 3.** Comparison of the number of beak openings from nests as a response toward playback stimuli between (A) VPs and (B) ORWs in the playback-to-adults experiment. The red points and whiskers represent mean and standard errors of the observed data, respectively. The black points represent the raw data, while treatments with same/different letters indicate nonsignificant ( $P \geq 0.05$ )/significant ( $P < 0.05$ ) differences in responses, respectively.



**Figure 4.** Comparison of leaving time from nests as a response toward playback stimuli between (A) VPs and (B) ORWs in the playback-to-adults experiment. The red points and whiskers represent mean and standard errors of the observed data, respectively. The black points represent the raw data, while treatments with same/different letters indicate nonsignificant ( $P \geq 0.05$ )/significant ( $P < 0.05$ ) differences in responses, respectively.

leaving time also differed among playback stimuli ( $\chi^2 = 493.9$ ,  $P < 0.001$ , marginal pseudo- $R^2 = 0.67$ , GLMMS; Figure 4B), and the response order was the same as for VP: first heterospecific distress calls (mean  $\pm$  SE =  $20.94 \pm 6.05$ ), followed by conspecific distress calls (mean  $\pm$  SE =  $22.56 \pm 5.52$ ) and then background noise (mean  $\pm$  SE =  $61 \pm 0$ ).

### Discussion

The results of the playback-to-chicks experiment revealed that both VP and ORW chicks would reduce the number of begging calls and begging duration as responses to distress calls of conspecifics and heterospecifics. This implied that VP/ORW chicks could eavesdrop



on threatening signals from nestmates, conspecific neighbor chicks, or even heterospecific chicks and react appropriately to decrease predation risk. However, for the number of beak openings, VP chicks did not show significant suppression, while ORW chicks reduced the beak opening frequency as a response to conspecific distress calls compared with other playback stimuli. Meanwhile, we tested the correlations of these 3 parameters of begging behavior of VP [begging duration – number of begging calls ( $r=0.77$ ); begging duration – number of beak openings ( $r=0.12$ ); number of begging calls – number of beak openings ( $r=0.19$ ); Spearman correlation] and ORW [begging duration – number of begging calls ( $r=0.9$ ); begging duration – number of beak openings ( $r=0.48$ ); number of begging calls – number of beak openings ( $r=0.57$ ); Spearman correlation]. Two possible reasons that are not mutually exclusive may contribute to explain this result. First, unlike acoustic signals such as the number of begging calls and persistent visual signals such as begging duration, the number of beak openings could be a purely short visual signal produced by chicks without sound. Emitting such a signal may be safer than using an acoustic signal or long visual begging, because the transmission of a visual signal would be blocked by vegetation, becoming less effective but more cryptic (Whittingham et al. 2004). For this prediction, we used Mann–Whitney  $U$  tests to determine whether both chicks would increase the number of beak openings to compensate for the suppression of acoustic communication. We found that chicks of VP did not increase the number of beak openings when presented with background noise, conspecific distress calls, or heterospecific distress calls ( $P > 0.05$ ), and chicks of ORW did not increase the number of beak openings when presented with heterospecific distress calls or background noise ( $P > 0.05$ ). Meanwhile, ORW suppressed the number of beak openings when presented with conspecific distress calls ( $P < 0.05$ ). In contrast, acoustic signals can be transmitted in dim light conditions and can travel long distances (Slabbekoorn and Smith 2002). Hence, begging calls increase the probability of being heard by a predator. Previous studies have found that in order to reduce predation risk, altricial chicks may suppress their begging calls in response to conspecific alarm calls uttered by parents (Barati and McDonald 2017). Because begging calls could increase predation risk (Chappell and Bachman 2002; Haskell 2002), VP chicks decreasing the level of acoustic signals while maintaining the visual signal intensity may indicate a tradeoff between the needs for suppression (to decrease predation risk) and begging (to acquire food). Second, unlike VP, conspecific distress calls reduced number of beak openings in ORW. This implies that ORW chicks may discriminate conspecific signals from other playback sounds. Moreover, ORW chicks are significantly larger than VP chicks, making their visual signals more conspicuous to predators.

The results of the playback-to-adults experiment showed that ORW parents reacted to distress calls uttered by both conspecific and heterospecific chicks compared with the control background noise. This indicated that the distress calls of chicks, as a type of alarm call, could carry information concerning danger to evoke parents' reactions such as leaving their nests. This result also indicated that ORW adults could eavesdrop on and react to the distress calls of conspecific neighbors and sympatric heterospecifics. Meanwhile, the nest-leaving behavior of ORWs did not differ significantly between the VP and ORW distress calls. This implied that ORW regarded the danger signals from conspecifics or sympatric heterospecifics as indicating the same level of threat or simply that they could not distinguish between these 2 distress calls. Additionally, there was no significant difference in the nest-leaving

behavior among the 3 playback stimuli for VP. Finally, the results of leaving time showed that the vigilance of both VP and ORW adults followed an order from ORW distress calls to VP distress calls. In other words, ORW adults responded to conspecific distress calls more quickly than to heterospecific distress calls, while VPs presented the opposite response. One possible explanation may be that the distress calls of ORW chicks may carry some special characteristics that were naturally more efficient in triggering the reactions of VP adults. Second, VP may prefer to freeze in place instead of escaping in response to distress calls from outside. Alternatively, ORWs had a larger population size, and this may make their distress calls a more common and representative signal for VPs. For future research, we suggest that if playback of distress calls comes from their own offspring, the parents would behave more aggressively in their anti-predator behavior.

Our results support the warn-kin hypothesis, that chicks would react to conspecific chicks' distress calls and reduced begging behavior. From the analysis of distress calls and spectrograms, we found that the distress calls were different in VP and ORW. In addition, we found that not only adults but also chicks would eavesdrop on heterospecific chicks' distress calls to avoid predation. Actually, the eavesdropping on heterospecific signals is a part of a mutualistic relationship (Magrath et al. 2015). In this wetland, VP and ORW share the same predators. Conveying conspecific signals and eavesdropping on heterospecific signals can reduce predation risk and enhance an individual's fitness. These results show that eavesdropping may not be acquired through learning but rather is a congenital behavior.

Avian reproductive success is affected by many factors, the main factor being nest predation (Martin 1993; Chappell and Bachman 2002; Fu et al. 2016; Guppy et al. 2017). Distress calls, as reliable vocal indicators of a predator, may constitute a communication channel in both parent–offspring and inter-offspring interactions. Taken together, our results confirmed most of our predictions, that is, chick distress calls play an important role in conveying risk and the conditions of the chicks to siblings and parents, evoking conspecific and heterospecific alert responses that would contribute to minimizing reproductive cost and enhancing individual fitness in the face of predation events.

## Acknowledgments

We thank the Forestry Bureau of Yongnian County, Hebei Province, China, for permission to undertake this study. We are grateful to Jiaojiao Wang and Laikun Ma for their assistance with fieldwork.

## Funding

Financial support was provided by the Hainan Provincial Natural Science Foundation of China (320CXTD437 and 2019RC189 to C.Y.) and the National Natural Science Foundation of China (31672303 to C.Y.).

## Ethical Note

The animal study was reviewed and approved by the Animal Research Ethics Committee of Hainan Provincial Education Centre for Ecology and Environment, Hainan Normal University.

## Authors' Contributions

C.Y. conceived and designed the study. Y.J., J.H., Z.Z., and X.C. performed the experiments. C.Y. and Y.J. analyzed the data and prepared the draft of

the manuscript. C.Y. improved the manuscript. All authors have read and approved the final version of the manuscript.

## Conflict of Interest

The authors declare no conflict of interest.

## Supplementary Material

Supplementary material can be found at <https://academic.oup.com/cz>.

## References

- Aubin T, 1991. Why do distress calls evoke interspecific responses? An experimental study applied to some species of birds. *Behav Process* 23:103–111.
- Barati A, McDonald PG, 2017. Nestlings reduce their predation risk by attending to predator-information encoded within conspecific alarm calls. *Sci Rep* 7:11736.
- Benedict L, 2007. Offspring discrimination without recognition: California towhee responses to chick distress calls. *Condor* 109:79–87.
- Bermant G, 1963. Intensity and rate of distress calling in chicks as a function of social contact. *Anim Behav* 11:514–517.
- Brémond JC, Aubin T, 1990. Responses to distress calls by black-headed gulls *Larus ridibundus*: The role of non-degraded features. *Anim Behav* 39:503–511.
- Caro T, 2005. *Antipredatory Defenses in Birds and Mammals*. Chicago (IL): The University Chicago.
- Carter G, Schoeppler D, Manthey M, Knörnschild M, Denzinger A, 2015. Distress calls of a fast-flying bat (molossid molossid) provoke inspection flights but not cooperative mobbing. *PLoS ONE* 10:e0136146.
- Chappell MA, Bachman GC, 2002. Energetic costs of begging behaviour. In: Wright J, Leonard M, editors. *The Evolution of Begging*. Dordrecht, the Netherlands: Springer, 143–162.
- Conover MR, 1987. Acquisition of predator information by active and passive mobbers in ring-billed gull colonies. *Behaviour* 102:41–57.
- Conover MR, 1994. Stimuli eliciting distress calls in adult passerines and response of predators and birds to their broadcast. *Behaviour* 131:19–37.
- Curio E, 1976. *The Ethology of Predation*. Berlin, Germany: Springer.
- De Toledo LF, Fernando C, Haddad B, 2009. Defensive vocalizations of Neotropical anurans. *S Am J Herpetol* 4:25–42.
- Driver PM, Humphries DA, 2008. The significance of the high-intensity alarm call in captured passerines. *Ibis* 111:243–244.
- Fenton MB, Belwood JJ, Fullard JH, Kunz TH, 1976. Responses of myotis lucifugus (Chiroptera: Vespertilionidae) to calls of conspecifics and to other sounds. *Can J Zool* 54:1443–1448.
- Froidevaux JSP, Roemer C, Lemarchand C, Martí-Carreras J, Maes P et al., 2020. Second capture of *Promops centralis* (chiroptera) in French Guiana after 28 years of mist-netting and description of its echolocation and distress calls. *Acta Amazon* 50:327–334.
- Fu Y, Chen B, Dowell SD, Zhang Z, 2016. Nest predators, nest-site selection and nest success of the Emei Shan liocichla *Liocichla omeiensis*, a vulnerable babbler endemic to southwestern china. *Avian Res* 7:1–6.
- Guo Z, Chen W, Hu J, 2006. Analysis on nest habitation factors and chick growth of *Paradoxornis webbianus*. *Sichuan J Zool* 25:858–861.
- Guppy M, Guppy S, Marchant R, Priddel D, Carlile N et al., 2017. Nest predation of woodland birds in south-east australia: importance of unexpected predators. *Emu* 117:92–96.
- Haff TM, Magrath RD, 2012. Learning to listen? Nestling response to heterospecific alarm calls. *Anim Behav* 84:1401–1410.
- Haskell DG, 2002. Begging behaviour and nest predation. In: Wright J, Leonard M, editors. *The Evolution of Begging*. Dordrecht, the Netherlands: Springer, 163–172.
- Högstedt G, 1983. Adaptation unto death: function of fear screams. *Am Nat* 121:562–570.
- Hörmann D, Tschapka M, Rose A, Knörnschild M, 2021. Distress calls of necrotrophic bats *Glossophaga soricina* encode individual and species identity. *Bioacoustics* 30:253–271.
- Koenig WD, Stanback MT, Hooge PN, Mumme RL, 1991. Distress calls in the acorn woodpecker. *Condor* 93:637–643.
- Laiolo P, Serrano D, Tella JL, Carrete M, Lopez G, Navarro C, 2007. Distress calls reflect poxvirus infection in lesser short-toed lark *calandrella rufescens*. *Behav Ecol* 18:507–512.
- Laiolo P, Tella JL, Carrete M, Serrano D, Lopez G, 2004. Distress calls may honestly signal bird quality to predators. *Philos T R Soc B* 271:S513–S515.
- Lamprecht J, 1985. Distress call alternation in hand-reared goslings *Anser indicus*: vocal co-operation between siblings? *Anim Behav* 33:839–848.
- Lingle S, Wyman MT, Kotrba R, Teichroeb LJ, Romanow CA, 2012. What makes a cry a cry? A review of infant distress vocalizations. *Curr Zool* 58: 698–726.
- Loth A, Frigerio D, Kotschal K, Szpl G, 2018. Differential responses to gosling distress calls in parental and non-parental greylag geese. *J Ornithol* 159:401–412.
- Ma L, Yang CC, Liang W, 2021. Nest-site choice and breeding success among four sympatric species of passerine birds in a reedbed-dominated wetland. *J Resource Ecol* 12:22–29.
- Madden JR, Kilner RM, Davies NB, 2005. Nestling responses to adult food and alarm calls: 1. Species-specific responses in two cowbird hosts. *Anim Behav* 70:619–627.
- Magrath RD, Haff TM, Fallow PM, Radford AN, 2015. Eavesdropping on heterospecific alarm calls: from mechanisms to consequences. *Biol Rev* 90: 560–586.
- Martin TE, 1993. Nest predation and nest sites. *Biol Sci* 43:523–532.
- Nakagawa S, Schielzeth H, 2013. A general and simple method for obtaining  $R^2$  from generalized linear mixed-effects models. *Methods Ecol Evol* 4: 133–142.
- Rendall D, Notman H, Notman MJ, 2009. Asymmetries in the individual distinctiveness and maternal recognition of infant contact calls and distress screams in baboons. *J Acoust Soc Am* 125:1792–2805.
- Roberto IJ, Botero-Arias R, 2013. The distress call of caiman *Crocodylus crocodylus* (Crocodylia: Alligatoridae) in western Amazonia, Brazil. *Zootaxa* 3647: 593–596.
- Rohwer S, Fretwell SD, Tuckfield RC, 1976. Distress screams as a measure of kinship in birds. *Am Midl Nat* 96:428–430.
- Ruiz-Monachesi MR, Labra A, 2020. Complex distress calls sound frightening: The case of the weeping lizard. *Anim Behav* 165:71–77.
- Slabbekoorn H, Smith TB, 2002. Bird song, ecology and speciation. *Philos T R Soc B* 357:493–503.
- Valone TJ, 2007. From eavesdropping on performance to copying the behavior of others: A review of public information use. *Behav Ecol Sociobiol* 62:1–14.
- Venuto V, Ferraiuolo V, Bottoni L, Massa R, 2001. Distress call in six species of africanpoicephalusparrots. *Ethol Ecol Evol* 13:49–68.
- Wang JJ, Yang CC, 2020. Specific responses of cuckoo hosts to different alarm signals according to breeding stage: A test of the offspring value hypothesis. *Curr Zool* 66:649–655.
- Wang Q, Yang C, Xiao H, 2013. The breeding ecology of oriental great reed warbler *Acrocephalus orientalis* in hongjiannao of Shaanxi province. *Sichuan J Zool* 32:543–546.
- Whittingham MJ, Butler SJ, Quinn JL, Cresswell W, 2004. The effect of limited visibility on vigilance behaviour and speed of predator detection: Implications for the conservation of granivorous passerines. *Oikos* 106: 377–385.
- Wise K, Conover MR, Knowlton FF, 1999. Response of coyotes to avian distress calls: Testing the startle-predator and predator-attraction hypotheses. *Behaviour* 136:935–949.
- Wu Y, Petrosky AL, Hazzi NA, Woodward RL, Sandoval L, 2021. The role of learning, acoustic similarity and phylogenetic relatedness in the recognition of distress calls in birds. *Anim Behav* 175:111–121.