Investigating how different classes of nest predators respond to the playback of the begging calls of nestling birds

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Research

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Abstract

Background

Begging brings benefits and costs for nestling birds: it can indicate their needs to their parents, but it can also be a cue used by predators to find the nest. The costs, like many variables related to nest predation, can be specific to what kinds of predators are present and their auditory capabilities. These costs and benefits could also be affected by human noise, as noise could disrupt communication to parents and eavesdropping by predators, although human-produced noise might be easily ignored if predators can hear high-frequency components of the begging. We studied nest predation on a generalist bird, the Red-whiskered Bulbul *Pycnonotus jocosus*, in a tropical rainforest in which there are many kinds of nest predators, including birds, mammals and reptiles.

Results

In a total of 160 artificial nests, we broadcast recordings of begging nestlings, with and without traffic noise, at two volume levels. We hypothesized that playback would increase predation relative to a silent control, and that mixing in traffic noise with the begging would decrease predation, as the begging signal was masked. However, we hypothesized that some predators, particularly small mammals with sensitive high-frequency hearing, might ignore the traffic noise. We found that predation was lowest for the control treatment, and lower for treatments mixed with traffic noise than for those without it. Small mammals, however, showed an unexpected pattern, strongly avoiding the treatments with traffic noise.

Conclusion

Our results demonstrate the human-associated noise can disturb nest predators and influence which kinds of predators use begging to locate nests.

Background

Nest predation is a major cause of mortality for birds, and hence has strongly shaped their life histories [1, 2]. Nest predation appears higher in tropical areas [3, 4], and also in human-disturbed habitats [5–8]. It is thus possible that anthropogenic change may lead to new predation threats for nestling birds and an overall threat to avian conservation [9]. However, there is a great degree of variability among different habitats and regions in their dominant nest predators, and so most meta-analyses of nest predation have struggled to find general patterns [5–8].

The effect of nestling begging on nest predation is a theoretically interesting question because, although it helps parents understand the nutritional needs of their young, begging also provides a way for nest predators to find nests [10]. Several playback experiments have shown that begging can increase exposure to nest predation [11–13], and the addition of loudly-begging nestling cuckoos to nests also can increase predation [14]. Birds have evolved to minimize the attraction of begging calls to predators; for example, ground-nesting birds, which generally have high nest predation, have higher frequency begging calls, which transmit less distance and hence are more difficult to detect [15].
Given the importance of nest predation to birds, and begging to nest predation, a crucial question is how begging activity, and predator response to it, is impacted by human disturbance. General adaptations of bird vocalizations to human disturbance are well-known. For example, birds have been shown to increase the frequency of their vocalizations in noisy conditions [16]. Animals may also increase the volume of sounds in noisy conditions, which is called a Lombard effect [17]. Indeed, a study on begging nestlings showed that nestlings increased the volume of their begging in noisy conditions (ambient noise in the field, white noise in laboratory tests) [18]. This research raises the question of whether it is possible that noise could make nestling birds particularly susceptible to predators. As human-made noise is generally at low frequencies (in most cases peaking below 1 kHz) [17], although there can be some high frequency components) [19] and begging can be at quite high frequencies (with considerable components above 6 kHz) [15], if nestling birds increase their begging volume in noise, nest predators that orient acoustically might detect more easily the increased volume at high frequencies where it is not masked.

We performed a playback experiment to look at the attraction of predators to begging calls and begging calls mixed with traffic noise at a study site with a great variety of predators (birds, mammals, and reptiles). We hypothesized that a) treatments that had the playback of begging would attract more predation than a control treatment (silence), b) playback at maximum volume (the highest amplitude of naturally recorded nestlings) would attract more predators than playback at mean volume, c) playback with traffic noise mixed with begging calls would attract fewer predators, because the begging calls would be partially masked. However, we predicted that when begging calls mixed with noise were played at maximum volume, the increase in volume would allow the animals to compensate for the masking, and that overall visitation rates to this treatment might approach that to the mean volume begging-only treatment.

Material

Study site

The study was conducted in and around the Nonggang National Nature Reserve (22°28'-22°30’N, 106°56’-106°58’E; elevation 59-215 m a.s.l.), using the nests of the Red-whiskered Bulbul *Pycnonotus jocosus*. Nonggang is a tropical limestone site, where researchers have spent a decade investigating the breeding ecology of the avifauna [20]. It is located in the southwest part of Guangxi Zhuang Autonomous Region, Southern China and has a tropical monsoonal climate [21]. The Red-whiskered Bulbul is abundant in buffer areas of the reserve which includes degraded forest, as well as plantations of sugarcane and the Chinese Chestnut (*Sterculia nobilis*), and its nesting has previously been studied in this area [22]. The species has also been studied in other tropical sites of southwest China, and been shown to attract a range of nest predators, including birds, mammals, and reptiles [23]. Its breeding season lasts about five months, from early April to late August, and we worked on this study throughout the breeding season, during three years, 2018-2020.

Measurements at the nests and recordings

We recorded begging calls at six nests in the buffer zone during May of 2018. We checked nests every two days, to document when the eggs hatched and hence the age of the nestlings. When nestlings were five days old and parents were not present at the nest, we positioned the end of a CR:152B model Cirrus Research sound level meter (SLM) about 1 cm close to the beak of the nestlings. The nestlings responded to this stimulus by
producing begging calls, as if in response to the parent [for similar behavior, see 24]. The SLM recorded 3 min of amplitude data, using its fast response setting and A weighting, with one data point collected every 1 s. The nestling calls’ fundamental frequencies were between ~ 4.5 and 6 kHz (Fig. 1).

At the same time as we recorded the amplitude of the vocalizations using the SLM, we also recorded those vocalizations using a K6 Sennheiser ME 62 omnidirectional microphone, placed 10 cm away from the nestlings, embedded in a Telinga parabola, and attached to a Marantz PMD 671 digital recorder. Recordings were made at 44,100 kHz sampling rate and in the .wav format. We then repeated this process when nestlings were 7 days old. We took care not to overly disturb the nest, and the whole recording process at a nest lasted only 10 minutes. Our manipulations did not appear to affect the success of the nests adversely, as four of six (66.7%) of the nests in which we worked fledged successfully, higher than the average success of nests in the area (nest success: 9/31 nests, 29.0%) [22].

In analyzing the SLM amplitude measurements, we found the difference between the amplitude when the chicks were begging (averaged across all such seconds), and the amplitude when the chicks were not begging (i.e. background noise), and calculated the amplitude of the begging [17]. We found no significant differences in amplitudes between the 5- and 7-day recordings. Pooling these two types of recordings together, we had 12 measurements of the amplitude of begging, averaging 73.1 ± 5.9 dB at 1 cm (hereafter referred to as “mean amplitude”). The loudest exemplar was 83.9 dB at 1 cm (hereafter referred to as “maximum amplitude”).

We placed an FHD-480 model RICH video camera at three nests to document typical parental behavior. According to the video cameras, we found the frequency of parental feeding was approximately 5-6 trips/hour, with the earliest feeding about 6:00 AM, and the latest about 6:00 PM.

**Noise selection and recording**

We selected traffic noise as the type of noise used in this study because it is the perhaps the most pervasive kind of anthropogenic terrestrial noise. We recorded traffic noise at close range because at this distance we found the high-frequency components to be considerable, so that they provided masking towards the lower frequencies of the begging of the bulbuls (i.e., around 4.5 kHz, Fig. 1). If nestling birds perceive some interference from traffic noise and increase their begging volume, as the experiments of Leonard ML and Horn AG [18] suggest they might, the higher frequency components of their vocalizations (e.g., 6 kHz and above) would not be as masked as their lowest frequencies (e.g. 4.5 kHz), and this might make them more vulnerable to predators that have sensitive high-frequency hearing.

We recorded traffic noise 5 m from large highways near Nanning, the capital city of Guangxi Zhuang Autonomous Region, using the same recording equipment as above, and with the microphone pointed into the flow of traffic. We made 6 separate recordings 3 km apart. Although the amplitude of the recordings was made so that it did not change over time, there were some fluctuations in the mix of frequencies on the recordings: the amount of energy above 4.5 kHz could be as high as ~ 1/10 of the total energy as a car approached, and less than ~ 1/50 when the cars were departing or distant.

**Design of playback tapes**
There were two kinds of playback treatments to prepare: begging tapes and the same begging sounds mixed with traffic noise. To make the begging tapes, we took the 1 min sections of the 3 min recordings with the greatest number of begging calls. Using Raven Pro (Version 1.5, Cornell Laboratory of Ornithology) we filtered the tapes (below 0.7 kHz), and edited them to get rid of background noises, while keeping the original repetition rate of the begging calls. To make the mixed tapes, we used Audacity (version 2.4.1, Audacity Team) to mix with any begging recording an equal amplitude of traffic noise, so that at peak amplitudes (i.e. when the chick called) the total amplitude of the mixed tape consisted of half begging and half traffic noise (as judged using the dimensionless units of amplitude [kU] in Raven Pro’s waveform display, see Fig. 1). Begging was partially masked by the traffic noise, although the majority of the power of the traffic noise was at lower frequencies. The masking effect had some fluctuation according to the approach and departure of the cars, with an approximately average situation shown in Fig. 1.

Playback tapes were then made that were 12 hours long, with a 1-min section of begging calls followed by 10 min of silence repeated many times to replicate the patterns that had been recorded by the videocameras. There were a total of five playback treatments: 1) begging played at mean volume (BEG), 2) begging played at maximum volume (BEGMAX), 3) mixed (begging calls + traffic noise) played at mean volume (the same volume as treatment 1, BEGNOISE), 4) mixed played at maximum volume (the same volume as treatment 2, BEGNOISEMAX), and the silent control (SILENT).

**Playback protocol**

Small speakers (AM1 Plus Abramtek speaker, China, which have an approximately flat frequency response curve between 100 and 10000 Hz) were hung 3-10 cm from the nest. Volume was controlled by adjusting the volume of the speaker so that it matched the mean amplitude (begging and noise at ~77 dB, with noise at ~75 dB, producing an amplitude of begging at ~73 dB, all assessed at 1 cm from the speaker) or the maximum amplitude (begging and noise at ~87 dB, with noise at ~84 dB, producing an amplitude of begging at ~84 dB, again at 1 cm from speaker) of the measurements of begging. Playback was started at 6 AM and played until 6 PM for seven straight days, with 5-day old nestling recordings used the first four days, and 7-day old nestling recordings used the last three days. On each day a playback exemplar (one of six) was chosen randomly, as long as it had not been used at that nest before.

In the beginning of the project (the 2018 field season), we conducted the experiment at nests that had been used that year. After the nestlings fledged or were predated, we waited one week, and then reused the nest, provided they were not damaged. Wearing plastic gloves, we first cleaned the nests of any excrement or egg shells. We then placed eggs made of plasticine in the nests. These eggs were made to mimic Red-whiskered Bulbul eggs in their size (approximately 16 mm X 22 mm) and coloring (marks were painted on the plasticine using waterproof paints). In addition to the speaker, we also placed at the nest an infrared camera (SG-660v, Shenzhen Siyuan Digital Technology Co., China) to detect predation events. This camera was always positioned slightly higher than the nest so that the eggs were visible, and was kept 0.5-1.0 m away horizontally.

A nest was considered to be predated if at least one egg was damaged or disappeared. Each nest was assigned to one treatment randomly, as long as nests with the same treatment were not within 250 m of each other. In the 2018 year, we used 20 such nests. A problem with the natural nests was that they were frequently damaged by rainfall, limiting the number of nests in which we could put the artificial eggs. In order to increase the sample
size, we used hand-made artificial nests, constructed out of dried twigs and vines to be of similar size and shape to the bulbuls’ nests and painted to resemble them. In 2018, we installed 40 of these artificial nests in locations where we had observed actual nests over the previous two years (in other projects), but where these nests had been damaged. The overall predation rate was similar to that of the natural nests (see results). We therefore used artificial nests in the last two years of the study (2019 and 2020, 100 nests), again placing them at places where real nests had been located that year. The birds did not reuse the same locations year-after-year.

Predators were identified if they: a) approached within 2 m of the nest on the day on which the nest was predated [11], and b) by bite marks on the plasticine eggs. In general, bite marks of small mammals showed small incisions from their teeth or a thin layer of the egg gnawed off (Fig. 2). In contrast, the beaks of the large predatory birds made wide, penetrating gouges into the artificial egg. If all the eggs disappeared at once without any pictures, we suspected a snake. If a nest was predated by the same species more than once, we only count one predation event. However, in the analyses of classes of predators, we do count multiple predation events if the species of predator were different (but such predation events by multiple predators occurred for only two nests).

**Statistical analysis**

To understand how treatment affected nest predation overall, we used the most detailed information available, the number of days the eggs in a nest were exposed and not predated. Because there was a maximum of seven days exposed, we expressed this number as a proportion of the maximum, and specifically, the response variable was a matrix, composed of two numbers for each nest: the days the eggs were exposed without predation ($D_p$) combined to (1-$D_p$). We then constructed a generalized linear mixed (GLM) model with a binomial distribution to understand the effect of playback treatment on this matrix, using the R statistical environment (R Core Team, 2021), base code. Results from this model were overdispersed, so we re-ran the model with a quasibinomial error structure, followed by Tukey HSD multiple comparisons. We then tested three planned contrasts corresponding to the three hypotheses: 1) whether predation was greater for the playback treatments, or the control, 2) whether predation was greater for maximum amplitude or mean amplitude, and 3) whether predation was greater for playback without traffic noise, or with traffic noise.

For understanding which predator classes (birds, mammals or reptiles) predated nests, we used a simpler, frequency table-based approach, as GLM models did not converge. For each of the three hypotheses we constructed a two-by-two table summarizing the number of nests predated or not predated by the predator class (with three classes being birds, mammals and reptiles), dependent on the characteristic of the playback (control vs treatment, amplitude, inclusion of traffic noise). We tested whether these tables showed evidence of differential response based on the characteristic of the playback with Fisher Exact Tests. We consider p-values < 0.05 significant.

**Results**

Predation of nests ranged between 1/2 and 2/3 of all nests across the three years (Table 1). In 2018, the predation of the natural, abandoned nests (10/20) was close to the predation of the artificial nests (21/40). Therefore, we used the artificial nests in further work and pooled together the results from natural and artificial nests.
nests. Predation in the years of 2019 and 2020 was somewhat higher (63/100) than predation in 2018, but not significantly so (Fisher's Exact Test, two-tailed, P = 0.34).

**Table 1.** Predation rate over three years and in natural and artificial nests.

| Predation rate (%)                        |
|-------------------------------------------|
| Treatment                                 |
|                                           |
| natural (n=4) artificial (n = 8) artificial (n=8) artificial (n=12) |
| Natural amplitude of begging calls (BEG) |
| 50 50 62.5 41.7                           |
| Maximum amplitude of begging (BEGMAX)    |
| 100 75 75.0 83.3                         |
| Traffic mixed with begging calls, natural amplitude (BEGNOISE) |
| 25 50 50.0 83.3                          |
| Traffic mixed with begging calls, maximum amplitude (BEGNOISEMAX) |
| 50 50 62.5 75.0                          |
| Silence                                  |
| 25 37.5 37.5 50.0                        |
| TOTAL                                    |
| 50 53 57.5 66.7                          |

**Table 2.** The kinds of predators identified in the study, and their relative attraction to the different treatments. Most of the predators were identified by the cameras (“photo”), although some were identified by bite marks. This list includes two nests that were attacked by multiple predators. Abbreviations for the birds: GRCO = Greater Coucal (*Centropus sinensis*); ICBM = Indochinese Green Magpie (*Cissa hypoleuca*); ABOW = Asian Barred Owlet (*Glaucidium cuculoides*). For reptiles, we identified one Asian Green Pit Viper (*Protobothrops mucrosquamatus*), one Chinese Green Tree Viper (*Trimeresurus stejnegeri*), and one Eastern Garden Lizard (*Calotes versicolor*).
The number of days that eggs in nests were exposed without predation was affected by playback treatment (Total deviance = 826.4, deviance associated with treatment = 64.5, p-value [using Chi-Square approach] = 0.0057). Eggs stayed unpredated longest in the silent treatment, and shortest in the BEGMAX treatment (Fig. 3). Multiple comparisons showed only these two treatments to be significantly different from each other (z = 3.26, P = 0.0098; although BEGMAX also tended to have quicker predation than BEGNOISEMAX, p = 0.072). Contrast 1 showed that predation was quicker for playback treatments, compared to the silent control (t = 2.38, p = 0.019). Contrast 2 showed that predation did not differ depending on volume (t = 0.02, p = 0.98). Contrast 3 showed that predation was quicker for treatments that did not have traffic noise (t= 2.21, p = 0.029).

Of the nine tests made to understand how different predator classes contributed to predation depending on the characteristics of the playback, only one was significant. Mammals came more to playbacks without traffic noise (14 depredation events) than to those with traffic noise (2 depredation events; two-tailed Fisher's Exact Test, P = 0.0023). While mammals avoided the traffic noise, birds came to the traffic noise treatments as much (19 times) as to the other playback treatments (15 times).

Discussion
Our results indicated that begging increased visits of nest predators to artificial nests in a community with several different kinds of nest predators. Using artificial nests has been found to give different results than natural nests in nest predation studies [25, 26], likely because the behavior of adults is lacking, either in attracting predators [27], or in warning their nestlings [28]. Our use of artificial nests must therefore be considered a limitation of the study. Nonetheless, we emphasize that many of the predators that were attracted to the nests (e.g. coucals, magpies, snakes, mice) are typical nest predators of our region (and from southern Yunnan, China [23]; see data from Thailand [29]). That begging attracts nest predators has also been shown in natural nests through playback [11], and by the addition of loudly-begging brood parasites [14]. Most studies of begging and nest predation have, however, involved only a few kinds of nest predators. Our study thus provides a useful assessment of how different classes of nest predators vary in the aural cues they use for detecting nests, and their response to human-associated noise.

We hypothesized that the different classes of predators would vary in their response to the treatments, with those with the best high-frequency hearing – small mammals – finding nests most sensitively. We indeed found a different between predator classes, but not that expected: mammals avoided traffic noise. The idea that mammals in particular might be repulsed by human presence (termed a “scarecrow effect”) by [30], has been suggested in some studies [31, 32] and meta-analyses [33]. Small mammals are also known to avoid roads [34], and noise in particular may influence their foraging decisions [35]. Another study completed in the same study area also showed much reduced nest predation in conjunction with human activity (specifically the photography of nests; Tan et al. in review).

This experiment was conducted in the buffer zone of a rainforest in which human noise is common, but large highway noise is not, and this may have been an important factor affecting our results. There was less (on average, though not significantly) nest predation in the BEGNOISEMAX treatment compared to the BEGNOISE treatment, perhaps suggesting that loud traffic noise was treated by the nest predators as particularly abnormal and repulsive (BEGNOISE playback sounded to the human ear like wind, whereas BEGNOISEMAX was more obviously traffic noise). For example, birds responded 12 times to BEGNOISE, but only 7 times to BEGNOISEMAX. In contrast, on average, and again not significantly, response to BEGMAX was higher than BEG (Fig. 3). These effects together meant that volume had no influence on response.

The low response of mammals to all traffic noise, and the reduced response of birds to BEGNOISEMAX, mean that we cannot fully evaluate our hypotheses as to how traffic noise might affect the responses of different classes of nest predators. We did not see any indication that an increased volume of begging mixed with noise would compensate for the masked signal, as we hypothesized. However, bird predators did respond to treatments of traffic noise as much as those without, showing that the partial masking by traffic noise of frequencies in the range of begging calls (greater than 4.5 kHz) posed little difficulty to them in detecting nests. We hope that the question of whether begging in noisy conditions might pose particular problems for nestling birds could be investigated in a more urban environment where nest predators like rats are not repulsed by traffic noise.

Our result that small mammals came less to treatments without noise is reminiscent of a growing body of work on how noise pollution can shift the composition of communities and species interactions. In a study of the effects of noise from industrial machinery, Francis CD, Ortega CP and Cruz A [36] found that an avian nest predator was adversely affected by the noise, with cascading effects on the populations of birds it predated.
This is apparently caused by the nest predator being less common in noisy areas. In our study, in comparison, the rodents are present in the area (as shown by them coming to the playback of begging only), but adverse to visiting nests when traffic noise was present. Further behavioral observations on how different classes of nest predators respond to noise is clearly warranted to understand the full conservation implications of human-produced noise [37].

Declarations

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Author contributions

Study concept and design: AJ, EG and SL. Acquisition of data: SL, QX and AJ. Wrote the manuscript: SL, QX, AJ and EG. All authors read and approved the final manuscript.

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Availability of data and materials

The authors will publish the data for the study upon acceptance, either as supplementary materials or on an online repository.

Ethical Statement

This research was approved by the Nonggang National Nature Reserve, by the Guangxi University Animal Ethics Committee (GXU2018-043), and followed the laws of the country in which it was conducted (People’s Republic of China). We followed the Guidelines to the Use of Wild Birds in Research [38], particularly in the selection of an abundant species on which to work, and a small number of individuals involved (audio recordings of six nests, video recordings of three nests). In recording the nestlings, we took pains to not disturb them long-term (10 minutes per nest per visit, two visits); videorecorded nests were only visited to install and pick up the equipment. In the playback trials, the predators were rarely attracted to the nest a second time, did not appear to digest the plasticine eggs, and therefore we believe their fitness was minimally affected.

Consent for publication

Not applicable.

Competing interests

The authors report no conflicts of interest.
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**Figures**
Figure 1

A representative waveform, spectrogram, and frequency spectrum of (A) the begging of Red-whiskered Bulbul nestlings, and (B) this same begging mixed with traffic noise recorded at close range. We mixed traffic noise into the tapes so that at the peak amplitudes of the tape the begging composed about half the amplitude, with the traffic noise contributing the other half. Subsequently the different tapes were standardized to the same playback volume.
Figure 2

Several of the predators at the nests, as recorded by the infrared cameras, and the damage they did to eggs. Here the interior of the egg is colored blue (using the photo editor, Adobe Photoshop), to make the pattern of bite marks on the artificial eggs clearer. Bite marks of small mammals showed small incisions from their teeth or a thin layer of the egg gnawed off whereas the beaks of the large birds made wide and deep gouges. The squirrel and mouse in panels (a) and (b) were unidentified to the species level. Panel (c) shows Indochinese Green Magpie (Cissa hypoleuca), panel (d) Greater Coucal (Centropus sinensis), and panel (e) Asian Barred Owlet (Glaucidium cuculoides). The speaker is visible in panels (d) and (e).
The number of days in that nests lasted undisturbed (out of a maximum of 7), for the different treatments. Treatments that have the same letter were not significantly different, using a generalized linear model, followed by Tukey HSD multiple comparisons. Sample size was 32 nests for each treatment.

Figure 3