ZOOLOGICAL RESEARCH

Responses of cuckoo hosts to alarm signals of different nest intruders in non-nesting areas

DEAR EDITOR,

The "call for help" hypothesis proposes that alarm calls produced by a bird can transmit warning information to both conspecific and interspecific neighbors. Neighbors who are attracted by social transmission might benefit from knowing about the presence of danger or by gaining information about the presence of predators or brood parasites nearby. Brood parasite hosts can distinguish threats from different intruders and exhibit varied responses correspondingly. However, most previous studies have conducted sound playback at host nest sites and focused on conspecific individuals attracted by the alarm calls. In this study, we used random location playback to investigate the responses of different host species to alarm signals of oriental reed warblers (*Acrocephalus orientalis*) toward different intruders (brood parasite, predator, and harmless control) in order to reveal how hosts evaluate different threats from different intruders using vocal information in non-nesting areas during the breeding season. We found that the alarm calls given in response to different intruders incurred similar numbers of approaching species for both conspecific and interspecific birds. However, the number of attracted individuals differed significantly among the various species, with conspecifics and vinous-throated parrotbills (*Paradoxornis webbianus*) dominating, both of which are major hosts of common cuckoos (*Cuculus canorus*). Nevertheless, interspecific birds did not present any aggressive behavior according to the alarm calls, which implied that visual information may be needed for further confirmation of threats. In addition, determining whether alarm call structure promoted an evolutionary convergence phenomenon still needs further verification.

Almost all birds, including those at the top of the food chain, are subject to some form of predation, resulting in birds evolving different anti-predation strategies depending on the threat posed by the predator (Marler, 2004; Suzuki, 2014, 2015). In addition, some birds are vulnerable to parasitic birds, which transfer the reproductive costs of nest building, egg tending, and nestling rearing to the host, leading to a significant reduction in host fitness (Davies, 2011; Soler, 2014). When the host encounters avian brood parasites or predators, it usually reacts with mobbing behavior and alarm calls, which not only attract intraspecific individuals but also members of interspecific species in order to successfully repel the intruder (Hurd, 1996; Welbergen & Davies, 2008; Yu et al., 2019a). Almost all birds use alarm calls as a key component of their anti-intruder response (Marler, 2004) to communicate important information on the presence of a threat.

To achieve successful nest defense and maximize fitness, hosts must first obtain information about the parasites (Yu et al., 2019a, 2019b). Generally, hosts can obtain relevant threat information in two ways: (1) newly obtained information from an individual, whereby individuals directly observe predators or other threatened individuals, and (2) social information, whereby individuals receive threat signals or cues from other individuals who have either observed threats or are aware of danger through social communication themselves (Dall et al., 2005). Sound signals can act in the dark, penetrate objects, and travel over long distances (Lemon, 1977; Slabbekoorn & Smith, 2002); when individual information is subject to certain visual constraints, sound communication becomes more valuable and therefore plays a very important role in the life history of birds (Whittingham et al., 2004). For example, northern cardinals (*Cardinalis cardinalis*) are more likely to flee when aerial calls of tufted titmice (*Baeolophus bicolor*) are played back than when a model of a titmouse is shown to them, possibly because invisible predators are more dangerous (Huang et al., 2012). This indicates that it is necessary to judge whether there is danger in the vicinity based on an audible signal, and the risk of predation would be

Received: 03 January 2020; Accepted: 20 March 2020; Online: 20 March 2020

Foundation items: This study was supported by the Hainan Provincial Natural Science Foundation of China (2019RC189 to C.C.Y.), National Natural Science Foundation of China (31672303 to C.C.Y. and 31970427 to W.L.), and Hainan Provincial Innovative Research Program for Graduates (Hyb2019-34 to J.J.W.)

DOI: 10.24272/j.issn.2095-8137.2020.030

greatly increased if the danger was judged by personal vision alone.

The alarm calls produced by birds can be used to attract both conspecific and interspecific neighbors; this has been referred to as the "calling for help" hypothesis (Hurd, 1996; Rohwer et al., 1976). Neighbors who are attracted by an alarm call may benefit from knowing about the presence of dangerous enemies or by gaining information about the presence of predators nearby (Grim, 2008). Signalers can also benefit. First, dilution of risk reduces the risk of injury for the individual. Second, attracting other species may be more effective in driving out invaders (Goodale & Ruxton, 2010). In some cases, information from interspecific species may be more reliable than information from conspecific individuals (Goodale & Ruxton, 2010; Seppänen et al., 2007). Studies have shown that various species, including birds, can recognize and respond to each other's alarm calls (Francis et al., 1989; Magrath et al., 2007; Marler, 1957; Seyfarth & Cheney, 1990; Vitousek et al., 2007; Walton & Kershenbaum, 2019). However, most research looked at alarm call warnings of predators, although a few studies have shown that certain species can recognize the information conveyed by conspecific or interspecific alarm calls about avian brood parasites; in addition, these studies conducted sound playback near nests and recorded the number and behaviors of conspecific species attracted by alarm calls (Walton & Kershenbaum, 2019; Yu et al., 2016, 2017a, 2017b, 2019a). Although other birds living in the same area may also be attracted by host alarm calls, playback of alarm calls of black-capped chickadees (*Poecile atricapillus*), for example, attracted at least 10 other species of birds with sympatric distribution. This suggests that species exposed to the same predator in the same area may benefit from recognizing each other's alarm calls; the unique feature of this playback experiment is that it used the old nests of tits (Hurd, 1996). In addition, Tryjanowski et al. (2018) used a random sampling method to attract up to 58 different species, both hosts and non-hosts, by playing cuckoo songs. However, further study is needed to determine whether the playback of alarm calls of avian brood parasites can also attract hosts or non-hosts when a specific nest is not targeted.

Here, we studied host responses to alarm signals of different intruders (brood parasite, predator, and harmless control) to investigate how hosts evaluate different threats from different intruders using vocal information in non-nesting areas during the breeding season. We used alarm calls from oriental reed warblers, a common host of common cuckoos, to three different intruders, including common cuckoos (brood parasite), sparrowhawks (*Accipiter nisus*, predator), and oriental turtle doves (*Streptopelia orientalis*, harmless control). We investigated responses to vocal signals by hosts, including oriental reed warblers and other potential host species that shared this information in a sympatric area. We predicted that (1) alarm signals may attract other sympatric species living in the same habitat as oriental reed warblers, but (2) the number of attracted oriental reed warblers may be greater than the number of attracted individuals of other species, and (3) the species that were attracted by the alarm call to cuckoos may also be recorded as hosts.

This study was performed in Yongnianwa National Natural Park, Yongnian District, Hebei Province (N36°40′60″–36°41′06″, E114°41′15″–114°45′00″). The average annual rainfall in this region is 527.8 mm, mainly concentrated in summer, and the average annual temperature is 12.9 °C. Reeds (*Phragmites australis*), cattails (*Typha latifolia*), and other herbaceous plants are the dominant flora in this wetland study area. The park experiences a temperate semi-humid continental monsoon climate. The Yongnianwa wetlands only stand at 40.3 m a.s.l., where water accumulates throughout the year. Oriental reed warblers that live and breed in reeds are the most common hosts of common cuckoos. Common cuckoos parasitize about 14.8% of all oriental reed warbler nests; this percentage is relatively stable and makes the social cues in the oriental reed warbler-cuckoo system a reliable source of information (Ma et al., 2018a, 2018b, 2019). Other common cuckoo hosts in a sympatric area include vinous-throated parrotbills, reed parrotbills (*Paradoxornis heudei*), blunt-winged warblers (*Acrocephalus concinens*), light-vented bulbuls (*Pycnonotus sinensis*), long-tailed shrikes (*Lanius schach*), and black drongos (*Dicrurus macrocercus*). Among these species, the first three live and breed in the same habitat as oriental reed warblers.

From the alarm calls recorded by the oriental reed warblers in response to observations of common cuckoos, sparrowhawks, and doves (Ma et al., 2018a), we selected nine samples with relatively little noise and recorded relatively clear audio. These included three alarm calls of oriental reed warblers given in response to sightings of common cuckoos, three in response to sparrowhawks, and three in response to doves. For the convenience of expression, hereinafter these are referred to as cuckoo, sparrowhawk, and dove alarm calls, respectively (Yu et al., 2017b). These sounds were imported into Raven Pro 1.4 sound analysis software, and as far as possible the overlapping sounds and low-frequency noises were removed; however, the original sound rate was held as unchanged as possible, and each was produced for 3 min of playback. The playback volume was about 75 dB at a distance of 1 m from the speaker (Yu et al., 2019a).

We performed playback experiments in a non-nesting area using random sample point locations (Tryjanowski et al., 2018) on sunny days during the breeding season from July to August 2017. Each sample point randomly received one playback sound (cuckoo, sparrowhawk, or dove alarm call). The playback dates did not differ significantly among playback locations of different alarm calls (F=0.086, df=2, P=0.918, Welch's ANOVA). The distance between each two adjacent sample points was at least 20 m, and any two adjacent points were not used for playback on the same day. A speaker (P2, Shidu Digital Technologies Inc., Shenzhen, China) was attached to a bamboo pole 1.5 m from the ground, and a digital video recorder (WJO3, HiSilicon Technologies Inc., Shanghai, China) was placed 5 m away from the speaker.

Playback occurred only if alarm calls of any bird were not heard or a predator was not seen for 5 min (Cunningham & Magrath, 2017), after which the selected test sound was used for playback. A total of 87 sample points (cuckoo alarm call: *n*=30; sparrowhawk alarm call: *n*=30; dove alarm call: *n*=27) were used for playback. The species, number of individuals, and response intensity within a radius of 5 m from the speaker were recorded during playback.

Statistical analysis was performed using SPSS 25.0 software for Windows (IBM Inc., USA). All statistical tests were two-tailed, with a significance level of $P<0.05$. Multiple analysis of variance (MANOVA) was used to test differences in the number of species attracted by the speakers when different alarm calls were played back. The dependent variable was the number of approaching individuals of different host species, the fixed factor was the playback stimulus (cuckoo, sparrow hawk, or dove alarm call from oriental reed warblers), and the covariate was the number of approaching species (number of species that approached the speaker). Among the species attracted by the alarm calls, all birds responded to the sounds by watching nearby, except for six cases of alertness recorded in oriental reed warblers (three to a dove alarm call; two to a cuckoo alarm call; and one to a sparrowhawk alarm call). As too few of these cases were available, no analysis was carried out to test host response intensity.

Seven species of birds were attracted by the alarm calls played back at random spots, namely the oriental reed warbler, vinous-throated parrotbill, reed parrotbill, blunt-winged warbler, light-vented bulbul, long-tailed shrike, and black drongo (Figure 1). All have been recorded as hosts of nest parasite cuckoos, with light-vented bulbuls and black drongos hosts of Indian cuckoos (*Cuculus micropterus*) and others hosts of common cuckoos (Yang et al., 2012, 2014b, 2015). The cuckoo alarm call attracted all above species, but the sparrowhawk alarm call did not attract black drongos and the dove alarm call did not attract black drongos or light-vented bulbuls (Figure 1). The MANOVA results showed a significant difference in the number of individual species responding to different alarm calls ($F=0.689$, df=2, $P=0.502$, MANOVA; Table 1), but the number of approaching species was a significant covariate ($F=107.683$, $df=1$, $P<0.001$, MANOVA; Table 1). The number of oriental reed warblers and vinous-throated parrotbills was much higher than that of other species among the approaching birds (Figure 1).

Alarm calls of various species can attract individuals of both intraspecific and interspecific species; to date, however, most past research has focused on alarm calls of a particular species to predators (FitzGibbon, 1989; Francis et al., 1989; Kalb et al., 2019; Kalb & Randler, 2019; Marler, 1957; Seyfarth & Cheney, 1990; Vitousek et al., 2007; Walton & Kershenbaum, 2019). Our study played back alarm calls of oriental reed warblers in response to sightings of a common cuckoo (parasite), sparrowhawk (predator), or dove. The alarm call playback experiment attracted seven species of birds with sympatric distribution, although the number of individuals of each species was significantly different, with more oriental reed warblers and vinous-throated parrotbills responding than individuals of other species. However, no differences were observed in the number of individual approaches for the three alarm calls. The attracted species may have linked the oriental reed warbler's alarm calls to the presence of danger. These attracted species may be important to the success of birds in defeating parasites and predators (Goodale & Ruxton, 2010).

Nest defense is the frontline anti-parasitism strategy used by host species; successful nest defense by hosts can effectively reduce brood parasitism (Feeney et al., 2012;

Table 1 Multivariate analysis of variance related to number of approaching individuals of different host species (dependent variable), playback stimulus (alarm call to cuckoo, sparrowhawk, or dove from oriental reed warbler; fixed factor), and number of approaching species (number of species that approach speaker during experiment; covariate)

Source	*F*	*df*	*P*
Corrected model	37.188	3	<0.001**
Intercept	1.769	1	0.187
Playback stimulus	0.040	2	0.960
No. of approaching species	107.683	1	<0.001**

**: $P<0.01$.

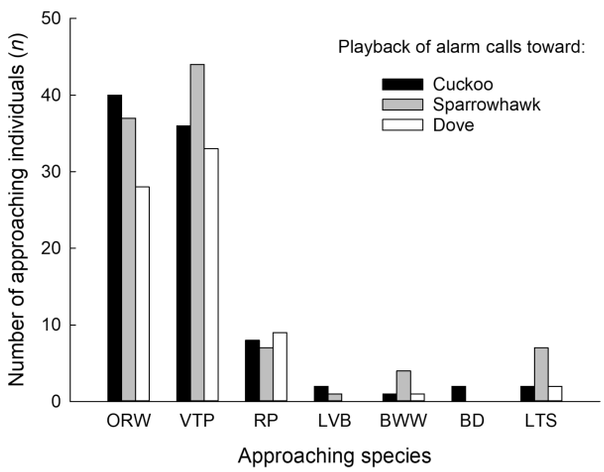

Figure 1 Number of approaching individuals of different species to playback of alarm calls from oriental reed warblers toward cuckoos (*Cuculus canorus*), sparrowhawks (*Accipiter nisus*), and doves (*Streptopelia chinensis*) in a random spot playback experiment (*n*=87 spots)

ORW: Oriental reed warbler (*Acrocephalus orientalis*), VTP: Vinous-throated parrotbill (*Paradoxornis webbianus*), RP: Reed parrotbill (*Paradoxornis heudei*), LVB: Light-vented bulbul (*Pycnonotus sinensis*), BWW: Blunt-winged warbler (*Acrocephalus concinens*), BD: Black drongo (*Dicrurus macrocercus*), LTS: Long-tailed shrike (*Lanius schach*).

Welbergen & Davies, 2009). In nest defense, alarm calls are a key component of the bird anti-intruder response (Marler, 2004); birds usually transmit alarm information about different threats to their mates or neighbors, and can recognize and respond to alarm calls from conspecific or heterospecific species with sympatric distribution (Hare et al., 2019; Yu et al., 2019a). These social messages can impact fitness by influencing certain life-history characteristics of the conspecific and heterospecific species (Campobello et al., 2015). In this study, heterospecific sound attraction was studied using random location playback of the alarm sound. Similarly, Tryjanowski et al. (2018) used the random spot method to attract up to 58 different species, both hosts and non-hosts, by playing back a cuckoo song. Although Hurd (1996) used old nests as sites to perform sound playback experiments on black-capped chickadees, their method was similar to random location playback and attracted 24 other species of birds. These studies, together with our own, suggest that non-nest-specific playback can attract a wider range of species than playback near nests, probably because random location playback increased the possibility of contact between birds and playback sound. However, random location playback rarely triggered aggressive behavior in these approaching species as most only approached the source of the sound and watched. This may have occurred because vocal signals attracted them at the beginning, but visual information was needed to confirm the subsequent reaction; it may also have something to do with local rates of parasitism (Welbergen & Davies, 2009). Furthermore, random location playback was not near a nest, so it may have been less threatening to the birds.

When compared with the other two studies, the calls used here attracted fewer species, possibly because species richness in this study area was lower than that in the other two regions. In addition, Tryjanowski et al. (2018) had visual stimulation when playing back cuckoo songs, which may have increased the number of attracted species. Hurd (1996) played back black-capped chickadee alarm calls of predators and found that the attracted birds included nest predators, which may have been attracted to find prey. In this study, species attracted by alarm sounds also included black drongos and long-tailed shrikes, two carnivorous birds that may also seek prey with sound. Interspecific attraction of alarm calls is thought to be a widely understood phenomenon, but some studies have shown that alarm calls attract interspecific birds only in specific areas. For example, Curio (1971) found that the playback of alarm sounds of European pied flycatchers (*Ficedula hypoleuca*) and collared flycatcher fantails (*F. albicollis*) attracted other species only in specific areas. In our study, the use of random location playback alarm calls maximally attracted other birds. Nevertheless, the playback attracted significantly different numbers of individuals of some species, with greater numbers of oriental reed warblers and vinous-throated parrotbills and fewer of other birds, which may be related to differences in host population density and territory in the study area. Oriental reed warblers, vinous-throated parrotbills, reed parrotbills, and blunt-winged warblers inhabit areas of reeds, whereas light-vented bulbuls, long-tailed shrikes, and black drongos inhabit forested areas. Furthermore, as a closely related species to great reed warblers (*Acrocephalus arundinaceus*), oriental reed warblers are also intensely parasitized by common cuckoos (Yang et al., 2014b, 2016, 2017). Although the parasitism rate for vinous-throated parrotbills by common cuckoos is low, coevolution has driven polymorphic eggs in both species due to disruptive selection (Yang et al., 2010, 2014a, 2015). Additionally, long-tailed shrikes and black drongos are larger in body size and fiercer than the other approaching species. Thus, all these reasons may explain the differences in the number of species approaching the speaker.

Nevertheless, although different species were attracted to the oriental reed warbler alarm calls, considering that most did not exhibit any aggressive behavior, the information encoded in the interspecific alarm calls by these species will need further study to verify its nature. In addition, if bird alarm calls are designed to prevent capture by a predator, in a specific area where the same predators exist, the alarm call structure of Passeriformes will experience evolutionary convergence (Marler, 1957); however, in this region, whether the structure of alarm calls constitutes an evolutionary convergence phenomenon still needs further verification.

SCIENTIFIC FIELD SURVEY PERMISSION INFORMATION

Permission for field surveys in Yongnianwa National Natural Park, Yongnian District, Hebei Province was granted by Forestry Bureau of Yongnian County, Hebei, China.

COMPETING INTERESTS

The authors declare that they have no competing interests.

AUTHORS' CONTRIBUTIONS

C.C.Y. conceived and designed the study. J.J.W. and L.K.M. performed the experiments. C.C.Y. and J.J.W. analyzed the data and prepared the manuscript. C.C.Y. and W.L. improved the manuscript. All authors read and approved the final version of the manuscript.

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