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Specific responses of cuckoo hosts to different alarm signals according to breeding stage: a test of the offspring value hypothesis

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Handling Editor: James Hare

Abstract

The selective pressure exerted by avian brood parasites forces their hosts to evolve specific defense strategies. When subject to brood parasite attack, avian hosts will often emit alarm calls. To date, few studies have examined whether and how host responses to different alarm calls indicative of different enemies vary with the host's breeding stage. We carried out alarm call playback experiments during both the egg and nestling stages of the oriental reed warbler *Acrocephalus orientalis*, a host of the common cuckoo *Cuculus canorus*. The playback exemplars were selected from recorded alarm calls of the warbler to the presence of common cuckoos, sparrowhawks *Accipiter nisus*, and oriental turtle doves *Streptopelia orientalis*, which represented brood parasite, predator, and harmless control, respectively. The results showed that the oriental reed warblers did not discriminate alarm calls issued to different intruder types, but the intensity of the response was significantly higher in the nestling stage than in the egg stage. Attack behavior related to sparrowhawk alarm calls was absent in the egg stage, but aggressive behavior increased dramatically and exceeded the attack frequency in response to the cuckoo alarm call in the nestling stage, implying a shift in the tradeoff between the parents' own survival and the loss of offspring. Alarm calls attracted a larger number of conspecifics than members of other species. In general, the oriental reed warbler had consistently stronger responses to different alarm calls in the nestling stage than in the egg stage, supporting the offspring value hypothesis.

Key words: brood parasitism, breeding stage, functionally referential calls, playback

Brood parasitism is a special reproductive behavior in which avian brood parasites lay eggs in other bird's nests and transfer the reproductive cost to the host ([Davies 2011](); [Soler 2014]()). The dynamics between parasite and host force hosts to develop a series of parasitism and antiparasitism strategies ([Davies 2011](); [Yang et al. 2020b]()). For the host, the defenses in the egg and chick stages are effective, but recognition errors can impose costs ([Stokke et al. 2016]()); in contrast, successful nest defense can increase host fitness without such risk ([Welbergen and Davies 2009](); [Feeney et al. 2012](); [Yang et al. 2020a]()).

In the nest defense stage, that is, when the host prevents its nest from being approached by parasites, hosts have evolved the ability to recognize the parasite, successfully inhibiting or reducing the cost of parasitism ([Davies and Brooke 1988](); [Langmore et al. 2009]()). At present, many researchers have tested whether hosts can respond in a specific way to parasites. Studies have found that some hosts can not only distinguish cuckoos from other threatening or nontatening species ([Duckworth 1991](); [Welbergen and Davies 2008](); [Trnka and Prokop 2012](); [Yang et al. 2014c](); [Li et al. 2015](); [Ma et al. 2018a](); [Yu

et al. 2019), but also adjust the strength of the nest defense according to the types of enemies and parasitism risk (Montgomerie and Weatherhead 1988; Caro 2005; Welbergen and Davies 2009; Campobello and Sealy 2010; Campobello and Sealy 2018). Furthermore, many species produce specific alarm calls in response to different threats (Grim 2005; Welbergen and Davies 2008), and birds are able to determine the type, size, speed, and behavior of an intruder based on conspecific or interspecific alarm calls, allowing them to respond appropriately and quickly (Evans et al. 1993; Templeton et al. 2005; Griesser 2008; Suzuki 2012; Soler 2014; Book and Freeberg 2015; Suzuki 2015; Thorogood and Davies 2016; Dawson Pell et al. 2018; Kalb et al. 2019; Kalb and Randler 2019; Yu et al. 2019). Japanese great tits *Parus major minor*, for example, produce "jar" calls to snakes and "chicka" calls to other predators such as crows and martens. The females respond to the "jar" calls by leaving the nest, but only observe the entrance to the nest when hearing the "chicka" calls (Suzuki 2014, 2015). The Siberian jay *Perisoreus infaustus* exhibited a specific flight response upon hearing conspecific alarm calls that conveyed threat information about predators (Griesser 2008). However, only a few studies of brood parasitism have examined the host's response to different alarm calls of conspecific individuals to different intruders.

In addition, parents should optimize their nest defense strategy based on the tradeoff between survival and the loss of nest contents (Montgomerie and Weatherhead 1988; Caro 2005). Previous studies have shown that the response to nest intruders by hosts varies according to the breeding stage (Barash 1975; Patterson and James 1980; Redondo and Carranza 1989; Duckworth 1991; Moskát 2005). For example, Duckworth (1991) showed that the reed warbler host had a strong, aggressive response to common cuckoo *Cuculus canorus* specimens during the egg stage, but when nestlings had fledged, the common cuckoo was largely ignored; the responses to jays *Garrulus glandarius* and sparrowhawks remained strong, regardless of the breeding stage. The responses of birds in these studies were influenced by the reproductive value of their offspring. The same was true of variation in the strength of the nest defenses of magpies *Pica pica* against humans (Redondo and Carranza 1989) and nonparasitic birds (Thornhill 1989). The offspring value hypothesis predicts that the nest defense level will be the highest during the nestling stage, as this is an adaptive response to the increased future value of offspring (Smith 1977). However, Ma et al. (2018a) found that oriental reed warbler *Acrocephalus orientalis* hosts demonstrated strong nest defense behavior, as they were very aggressive to nest intruders in both the egg stage and the nestling stage. Under visual stimulation, 90% of the oriental reed warblers attacked intruders and recruited conspecific helpers to participate in the attack. All of these studies examined how birds responded to visual models of parasites or predators according to breeding stage.

Birds generally respond similarly to alarm calls as they do to visual stimuli of the predators (Gill and Bierema 2013), with some exceptions (Liang and Møller 2015; Yu et al. 2017b; Adams and Kitchen 2020). For example, there were no differences in responses of barn swallows *Hirundo rustica* or great tits to cuckoo versus sparrowhawk models that presented visual stimuli only (Liang and Møller 2015; Yu et al. 2017b), but the 2 species could be distinguished by alarm calls, indicating that the alarm calls transmitted information about threat types (Yu et al. 2016; Yu et al. 2017b). The contrasting results obtained from experiments presenting visual stimuli and playback of some studies may be due to certain behaviors of the host to the threatening species being ignored during analysis of results from studies presenting visual models; therefore, it is

very important to use audio playback experiments to verify the results, because enemies are not always detected. They are often cryptic and hidden (Thorogood and Davies 2016). Although there have been a handful of studies that have used alarm calls for playback, these studies have been conducted only during the egg stage (Yu et al. 2016; Yu et al. 2017a; Yu et al. 2019). Therefore, there is a lack of research employing alarm call playback to verify whether birds discriminate nest parasites from other invaders by auditory signals alone, and whether the response also varies with different host breeding stages.

In this study, we examined oriental reed warbler *A. orientalis* responses to alarm signals for different intruders (brood parasites, predators, and harmless controls) to investigate how hosts evaluate threats posed by different intruders, and whether any differential response to those threats varies among stages of the host breeding cycle. According to the offspring value hypothesis, we predicted that oriental reed warblers would exhibit more aggression to sparrowhawk alarm calls during the nestling stage than in the egg stage, but the response to the cuckoo alarm calls would be the opposite, with enhanced response to cuckoo-specific alarm calls during the egg stage. Furthermore, because different intruders present different threats, we predicted that the aggression intensity should be lowest to the harmless intruders (i.e., doves), and the attack frequency should be lower to sparrowhawks than to cuckoos despite their apparent resemblance (Davies and Welbergen 2008), because the former are predators of adult birds.

Materials and Methods

Study site and subjects

The study area is located in Yongniwa National Natural Park, Yongnian district, Hebei province (36°40′60″–36°41′06″N, 114°41′15″–114°45′00″E). This area has a temperate semi-humid continental monsoon climate. The Yongniwa wetland is only 40.3 m above sea level and has standing water throughout the year, making it difficult to navigate. The average annual rainfall in this region is 527.8 mm, which mainly occurs in summer; the average annual temperature is 12.9°C. Reed *Phragmites australis*, cattail *Typha latifolia*, and other herbaceous plants are the main vegetation in the wetlands. The oriental reed warblers are hosts of the common cuckoos. Previous studies have found that the warblers can visually distinguish the common cuckoos from predators such as sparrowhawks *Accipiter nisus* and harmless species such as oriental turtle doves *Streptopelia orientalis* (Ma et al. 2018a). The probability of the oriental reed warbler being successfully parasitized by the common cuckoo is about 14.8% (Ma et al. 2018b).

Production of playback sounds

Audio recordings of alarm calls emitted by oriental reed warblers in response to taxidermic mounts of 3 species (common cuckoos, sparrowhawks, and oriental turtle doves) were employed in egg stage experiments performed in 2016, using a recorder (Lotoo L300E) connected to a shotgun microphone (Sennheiser MKH418) to record alarm calls emitted by hosts. The sampling frequency was 44.1 kHz, and the sampling resolution was 24 bits. The audio recordings of alarm calls with less noise from the mount presentation experiment were selected as the playback stimuli (Ma et al. 2018a).

To avoid pseudoreplication, we chose 3 nests for each type of sound (3 oriental reed warblers responding to the common cuckoo, later referred to as the cuckoo alarm calls; 3 oriental reed warblers

responding to the sparrowhawk, later referred to as the sparrowhawk alarm calls, and 3 oriental reed warblers responding to the oriental turtle doves, later referred to as the dove alarm calls; Yu et al. 2017b). We did not specifically use background noise as a control stimulus to playback to the oriental reed warbler nest, but we have played back noise to other host species in the same area where there were oriental reed warbler nests. During the noise playback, no birds, including oriental reed warblers, were attracted (Wang unpublished data). Raven Pro 1.4 software was used to clip the sound and remove noise $<0.2\,kHz$, and overlapping sounds (from the beginning of the overlapping element to the beginning of the next element) or sounds of other birds were deleted. We tried not to change the syllable type or call rate. Then, the high-quality alarm calls of parent birds were combined for 3 min to construct a playback stimulus (cuckoo alarm calls: 5.90 ± 2.41 notes/s; sparrowhawk alarm calls: 11.12 ± 3.01 notes/s; dove alarm calls: 11.64 ± 2.20 notes/s). Finally, we saved the audio files in Wavefom format. Each set of sounds was played at the same sound pressure level $(75\,dB\ SPLA\ ^{@1\,m})$, which is close to its natural level (Yu et al. 2019).

Playback experiments

Alarm call playback experiments were conducted in the egg stage (egg incubation stage, days after clutch completion: 2.30 ± 0.15 (mean $\pm$ SE) days; $n = 23$ and the nestling stage: 4.0 ± 0.23 (mean $\pm$ SE)-day-old nestlings, $n = 11$) of oriental reed warbler nests from June to July in both 2017 and 2019. The areas of observed nests between 2017 and 2019 rarely overlapped, and most host individuals from observed nests of 2017 wore colored rings, whereas none of the birds wore colored rings in 2019. We, therefore, consider the probability of pseudoreplication to be very low. Playback was not conducted in the same nest for both stages (i.e., 1 nest received 1 breeding stage playback). When the parent birds were not around the nest, 1 researcher (Laikun Ma or Jiaojiao Wang) quickly placed a Bluetooth speaker (BV370, China) at a distance of 1 m from the nest, and at a height same as the nest itself. A digital video camera (Sony, HDR-PJ510E, Japan) was placed 5 m away from the nest. The observers hid behind vegetation ∼5 m away to control the playback. Playback occurred only if natural alarm calls were not heard and an intruder was not seen for 5 min (Cunningham and Magrath 2017). In sunny day, playback experiments were conducted from 8:00 AM to 5:00 PM (BT) every day. Three sounds were played back at each nest for a duration of 3 min. The order of playback was random, and the interval between the presentation of the 2 playback exemplar types was at least 1 h. Playback at the same nest was performed on the same day; no neighboring nest received playback on the same day (Yu et al. 2016; Yu et al. 2017b). We recorded the species and number of birds that approached during playback within a

radius of 5 m from the speaker as well as the highest level of response intensity of all attracted birds. The responses were ranked on a scale of 1–4 to represent aggression in order from lowest to the highest: watching (score = 1), where birds only waited and observed within 5 m of the speaker without any noticeable reaction; alert (score = 2), birds were alert only at a safe distance $(>1\,m)$; mobbing (score = 3), where birds produced the alert and showed signs of attack on the speaker but did not come into contact with it; and attack (score = 4), body contact with the speaker, hitting the speaker as the bird flies over or stands above it pecking the speaker (Linhart et al. 2012). Each time we did a playback experiment, we used GPS to record the location, so that the playback trials did not overlap in either space or time. We did not distinguish between parasitized and nonparasitized nests in the playbacks, but included this as a variable in conducting our analyses.

Statistical analyses

We used general linear mixed models (GLMMs) to analyze the differences in the host response to different playback stimuli and different stages of the reproductive cycle. The response variable was the response to alarm calls by hosts. Nest identity was a random effect, whereas playback stimulus (cuckoo alarm call, sparrowhawk alarm call, or dove alarm call) and breeding stage (egg or nestling stage) were fixed factors. The effects of playback order, clutch size, egg-laying date (representing date in the breeding season), parasitism status (parasitized or unparasitized), the interaction between the playback stimulus and breeding stage, or playback order and breeding stage were also tested. If the fixed effects were significant, a post hoc test (sequential Bonferroni) was used for pairwise comparisons. We also calculated Cohen's d-value and its 95% confidence interval (CI) as the estimate of effect size for the significant predictors. A multivariate analysis (MANOVA) tested the differences in the numbers of approaching individuals that were attracted when different alarm calls were played back. The response variable was the number of approaching individuals, and the fixed effects included playback stimulus (cuckoo alarm call, sparrowhawk alarm call, or dove alarm call), approaching species (number of species that approached the speaker), and breeding stage (egg or nestling stage). The interaction between playback stimulus and approaching species and the interaction between the breeding stage and approaching species were also tested. The statistical analysis was performed using SPSS 25.0 for Windows (IBM Inc., USA). All statistical tests were 2-tailed, with a significance level of $P < 0.05$.

Results

The different alarm calls of oriental reed warblers attracted 3 species, the oriental reed warbler, the vinous-throated parrotbill

Table 1. Relative frequencies (%) of responses toward different playback stimuli by oriental reed warblers in nest playback trials according to the breeding stage

Effects	Egg stage ($n = 23$ nests)				Nestling stage ($n = 11$ nests)				Contrast of responses[a]			
	Watch	Alert	Mobbing	Attack	Watch	Alert	Mobbing	Attack	Watch	Alert	Mobbing	Attack
Alarm to cuckoo *C. canorus*	17.39	56.52	13.04	13.04	36.36	36.36	0	27.27	+18.97 ↑	−20.16 ↓	−13.04 ↓	+14.23 ↑
Alarm to sparrowhawk *A. nisus*	47.62	42.86	9.52	0	27.27	36.36	0	36.36	−20.35 ↓	−6.49 ↓	−9.52 ↓	+36.36 ↑
Alarm to dove *S. orientalis*	47.83	52.17	0	0	30.00	50.00	0	20.00	−17.83 ↓	−2.17 ↓	0	+20.00 ↑

[a] Contrast of responses refers to the changes of relative frequencies of responses from egg stage to nestling stage, in which the increase or decrease was labeled by ↑ or ↓, respectively.

Paradoxornis webbianus, and the reed parrotbill *P. heudei*. All 3 species are parasitized by the common cuckoo (Yang et al. 2014a, 2014b, 2015). However, only the oriental reed warbler responded to the playback with alert, mobbing, or attack (Table 1); for the 2

Table 2. Generalized linear mixed models used to predict the response (watch, alert, mobbing, or attack) to alarm calls (i.e., response variable) toward the playback stimulus (conspecific alarm call toward cuckoo, sparrowhawk, or dove), breeding stage (egg incubation or nestling stage), playback order, egg-laying date, clutch size, parasitism status (parasitized or unparasitized), and the interactions between several factors

Effects	F	df1	df2	P
Playback stimulus	2.461	2	86	0.091
Breeding stage	11.365	1	86	0.001
Playback order	0.930	2	86	0.398
Clutch size	0.769	1	86	0.383
Egg-laying date	2.226	1	86	0.139
Parasitism status	1.581	1	86	0.212
Breeding stage × Playback stimulus	0.758	2	86	0.472
Breeding stage × Playback order	0.291	2	86	0.749

Table 3. MANOVA of variance comparison of the approaching number of individuals from different host species (i.e., dependent variable) by the playback stimulus (alarm call to cuckoo, sparrowhawk, or dove from the oriental reed warbler), approaching species (oriental reed warbler, vinous-throated parrotbill, and reed parrotbill), breeding stage (egg incubation or nestling stage), and the interactions between factors

Effects	F	df	P
Playback stimulus	2.139	2	0.199
Approaching species	103.200	2	<0.001
Breeding stage	23.162	1	0.003
Breeding stage × Approaching species	12.655	2	0.007
Playback stimulus × Approaching species	0.314	4	0.859

parrotbill species, only watching behavior was recorded. According to the GLMM, the response intensity of the oriental reed warblers to different alarm calls was not significantly different ($F_{2,86} = 2.461$, $P = 0.091$, GLMM; Table 2). However, the response intensity of the warblers was higher in the nestling stage than in the egg stage ($F_{1,86} = 11.365$, $P = 0.001$, GLMM; Cohen's $d = 0.496$, 95% CI = -0.923 and -0.069; Table 2). In the egg stage, the oriental reed warbler attacked the speaker only if the cuckoo alarm calls were played back, and in the nestling stage, regardless of which kind of alarm calls were played back, there were attack behaviors toward the speaker. In addition, compared with the egg stage, the attack behavior of the warblers to cuckoo alarm calls increased during the nestling stage (Table 1). Additionally, there were no statistically significant results for other effects or interactions (Table 2). The number of individuals approaching the loudspeaker varied significantly among species ($F = 103.2$, df = 2, $P < 0.001$, MANOVA; Cohen's $d = 3.570$, 95% CI = 2.047 and 5.094; Table 3), but did not differ among playback stimulus types ($F = 2.139$, df = 2, $P = 0.199$, MANOVA; Table 3). However, there was a significant difference in the number of approaching individuals between the egg stage and nestling stages ($F = 23.162$, df = 1, $P = 0.003$, Cohen's $d = 0.582$, 95% CI = -0.361 and 1.525; MANOVA; Table 3), and there was an interaction effect between the approaching species and the breeding stage ($F = 12.655$, df = 2, $P = 0.007$, MANOVA; Table 3). Therefore, the number of individuals of the 3 responding species attracted by playback in the egg stage was higher than that in the nestling stage (Figure 1).

Discussion

The results of playback experiments revealed that the responses of oriental reed warblers to different alarm calls did not vary according to the species indicated by the call, suggesting that the hosts did not respond differentially to different intruder types. However, the intensity of the host response during the nestling stage was significantly higher than that in the egg stage. Although cuckoos seem to be more dangerous during the egg stage than the nestling stage, oriental reed warblers responded more aggressively toward cuckoo alarm calls in the nestling stage than in the egg stage, implying that
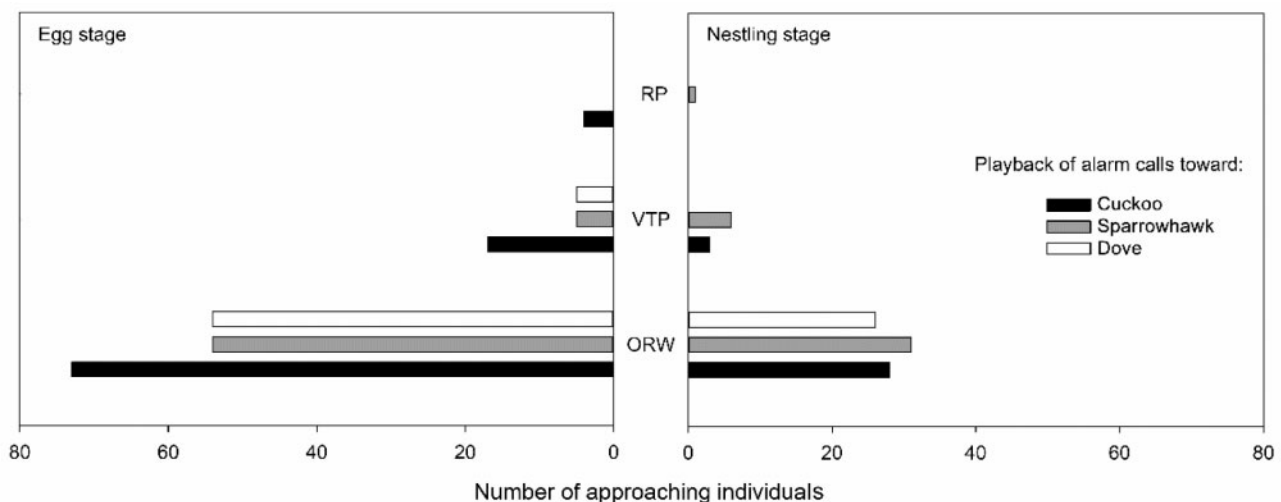

Figure 1. Number of approaching individuals of the oriental reed warbler (ORW) *A. orientalis*, vinous-throated parrotbill (VTP) *P. webbianus*, and reed parrotbill (RP) *P. heudei* to the playback of alarm calls from the ORW toward cuckoos *C. canorus*, sparrowhawks *A. nisus*, and doves *S. orientalis* between the egg ($n = 23$ nests) and the nestling ($n = 11$ nests) stages.

cuckoos are also recognized as dangerous nest predators. Although we found no evidence of common cuckoo predation upon host nests in this study, we did note this in other oriental reed warbler populations (unpublished data), and previous studies have also found that some cuckoo species, including common cuckoos, prey on host nests (Davies and Brooke 1988; Soler et al. 1995; Su et al. 2017). No attack behavior was identified toward sparrowhawks or doves in the egg stage; however, it did occur in the nestling stage, and its frequency significantly increased at more than double the rate of increase compared with that for the cuckoo alarm call. This implied that the evaluation of the same signal information by the host may dramatically change with different breeding stages, probably because the quantity of investment in offspring varying between different breeding stages changes the tradeoff between the loss of offspring and the survival of the adults themselves.

In the face of danger, hosts not only display behavioral responses but also produce alarm calls to attract partners and neighbors to jointly resist the intruder (Welbergen and Davies 2008). For the hosts, their ability to distinguish between different intruders and recognize conspecific alarm call information is important to successful nest defense (Caro 2005; Davies 2011), which directly improves their fitness. However, the results of a previous study with pairwise taxidermic mount presentation experiments revealed that oriental reed warblers failed to distinguish cuckoos from sparrowhawks (Ma et al. 2018a). Similarly, our playback experiments found no significant difference between the responses to alarm calls toward cuckoos or sparrowhawks, suggesting that the hawk mimicry of cuckoos was effective in deceiving oriental reed warblers. Additionally, the host response to doves was slightly less aggressive than that toward cuckoos or sparrowhawks without significant difference, which implied that this warbler species was sensitive to any intruder.

The threat-related information transmitted by acoustic signals has been verified in many species (Linhart et al. 2012; Suzuki 2012; Kleindorfer et al. 2013; Suzuki 2014, 2015; Kalb and Randler 2019). However, most of the research on alarm call playback has only focused on predators. In brood parasitism research, there are only a few studies of alarm call playback for parasites (Yu et al. 2016; Yu et al. 2017a, 2019), especially those about whether the host's nest defense behavior changes with the breeding stage. In this study, we used alarm calls to perform playback experiments simultaneously in the egg and nestling stages to test whether the response of host is consistent. As we predicted, the response of oriental reed warblers to different alarm calls was consistently more aggressive in the nestling stage compared with that during the egg stage, which supports the offspring value hypothesis (Smith 1977). Compared with the egg stage, parental birds invested relatively more energy in the nestling stage, presumably owing to the fact that the protection of nestlings determines whether reproduction will be successful. At this time, the birds should show aggressive behavior toward any intruder that appears near the nest. The behavior of attacking the speaker may be a manifestation of the host recognizing that the sound alone indicates a high threat level (Linhart et al. 2012).

We found that the numbers of attracted individuals did not differ among different playback stimuli, which is at odds with the findings of other studies where differences in host responses to cuckoos or cowbirds versus other threatening species were evident (Duckworth 1991; Neudorf and Sealy 1992; Hobson and Villard 1998). For example, reed warblers were more attracted by mobbing calls, and the higher repetition rate of mobbing syllables attracted more individuals (Welbergen and Davies 2008). However, the playback of all 3 types of alarm calls in both the egg and nestling stages attracted many more oriental reed warblers than individuals of other species, indicating that the alarm calls contained specific information for conspecifics. The oriental reed warblers and black-browed reed warblers *A. bistrigiceps* of the Heilongjiang population were able to recognize the threat level of each other's alarm calls and respond appropriately (Yu et al. 2019), as other studies have reported (Dawson Pell et al. 2018; Walton and Kershenbaum 2019). Although our study found that the alarm calls of the oriental reed warbler attracted birds of other species, whether they could correctly discern the information from interspecific alarm calls remains to be studied. Additionally, the total number of individuals attracted by playback in the egg stage was higher than that in the nestling stage. Although the attracted neighbors may benefit from knowing the presence of dangerous enemies (Grim 2008), some experienced species may have already reproduced when the playbacks occurred in the nestling stage; at such times, it would be unnecessary for neighboring birds to approach the source of the alarm calls, as this might increase the risk of being preyed upon. Alarm calls broadcast during the nestling stage may thus attract fewer birds.

In summary, the results of this study generally conformed to our prediction that the hosts would react consistently to all playback stimuli, and that responses would become more aggressive in the nestling stage compared with the egg stage. However, the aggression toward sparrowhawk alarm calls, including attack behavior, was not lower than toward cuckoo alarm calls, even though sparrowhawks are purportedly a dangerous predator of adult birds. Taken together, our results support the offspring value hypothesis.

Acknowledgments

Funding

Authors' Contributions

C.Y. designed the study, carried out laboratory, and statistical analyses. J.W. performed field experiments. C.Y. and J.W. wrote the draft manuscript and approved the final submission.

Conflict of Interest

The authors declare that they have no competing interests.

Ethical Standards

The experiments comply with the current laws of China. Fieldwork was carried out under the permission from the Yongniwa National Natural Park.

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