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Defensive adaptations to cuckoo parasitism in the black-browed reed warbler (*Acrocephalus bistrigiceps*): recognition and mechanism

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Abstract

Hosts of avian brood parasites suffer a high cost of reproductive loss due to parasitism, driving them to evolve a variety of anti-parasitic defenses. These defenses comprise a series of components, including the recognition of brood parasites and the eggs laid by the parasites, cues used for recognition, and the mechanisms on which these behaviors are based. In this study, we conducted egg recognition and nest intruder experiments to examine these components of anti-parasitic behavior in the black-browed reed warbler (*Acrocephalus bistrigiceps*), a rare host of the common cuckoo (*Cuculus canorus*). We found that the host possessed strong recognition capacity, rejecting 100% of parasitic eggs, and used a template-based mechanism for egg recognition. The host birds also rejected 80% of their own eggs on which artificial markings were added to the blunt pole; however, they accepted all eggs with the same manipulation on the sharp pole, implying that the blunt pole was an important recognition cue. Furthermore, the host exhibited stronger aggression to cuckoos than to harmless controls; a behavior specific to the incubation stage rather than the nestling stage. Therefore, the host was able to distinguish the cuckoo from other nest intruders as being a brood parasite. These results together help explain the near absence of cuckoo parasitism in black-browed reed warblers and provide new information concerning anti-parasitic defenses in this host species.

Keywords *Acrocephalus orientalis* · *Cuculus canorus* · Egg rejection · Recognition cue · Multiple egg parameters

Introduction

In the co-evolutionary system of avian brood parasitism, parasites initially cause significant reproductive losses in the hosts, thereby causing selection for the evolution of a series of anti-parasitic defenses to counter the former (Davies 2000; Soler 2014). For most host species, one of the most common and effective defenses against brood parasitism is the recognition and rejection of parasitic eggs (Davies 2011). To accurately reject foreign eggs, the hosts need to distinguish them from their own clutches; in response, the parasites may evolve mimetic eggs that make the rejection process difficult (Kilner 2006; Spottiswoode and Stevens 2010). Furthermore, the rejection rates vary among different host species and populations (Stokke et al. 2005). The seemingly simple behavior of egg rejection may depend on complex cognitive decision-making processes that involve one or multiple cues such as egg color, egg pattern, ultra-violet reflectance, and egg sizes or shapes (Rothstein 1982; Avilés et al. 2006; Antonov et al. 2010; Ruiz-Raya et al. 2015; Hanley et al. 2019; Hauber et al. 2019; Nahid et al. 2021).

Because avian eggs of many bird species are covered with patterns, one of the egg characteristics that has received attention is the pattern distribution on different parts of the egg. As is well known, bird eggs are notable for their specialized shapes; the eggshell can be divided into a sharp pole and a blunt pole. Generally, most large markings are concentrated on the blunt poles of eggshells (Lack 1968; Kilner 2006). Polačiková et al. (2007) found that egg recognition

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in hosts may focus on specific positions of the eggshells and suggested the blunt egg pole hypothesis, i.e., that pattern distribution and color variation on the blunt pole of eggs is an important cue for egg discrimination by hosts (Polačiková et al. 2007, 2010; Polačiková and Grim 2010). To date, this hypothesis has been experimentally confirmed in some hosts, and it applies to both maculate and immaculate host eggs (Polačiková et al. 2010; Polačiková and Grim 2010; Wang et al. 2020a, b). However, negative results were found in the American robin (*Turdus migratorius*) host (Hauber et al. 2021).

Nevertheless, the cognitive response to the parasitic eggs by hosts is not only related to the recognition cues mentioned above but also involves the proximal mechanism of egg recognition. There are two widely discussed hypotheses concerning the mechanism of egg recognition by hosts: 1) true or template-based recognition, which holds that the hosts use their own eggs as a recognition template through innate ability or re-learning; and 2) recognition by discordance, which states that recognition does not rely on a template or learning but is based on the relative number of eggs, in that the hosts regard the eggs in the minority as parasite eggs (Rensch 1925; Rothstein 1974, 1975; Hauber and Sherman 2001; Yang et al. 2014; Tosi-Germán et al. 2020). At present, most findings support the true or template-based recognition hypothesis (Lyon 2007; Bán et al. 2013; Lang et al. 2014; Tosi-Germán et al. 2020; Yi et al. 2020; Ma and Liang 2021), while a combination of the two recognition mechanisms has also been confirmed in some studies (Moskát et al. 2010; Yang et al. 2014).

In this study, we conducted egg recognition and nest intruder experiments in the black-browed reed warbler (*Acrocephalus bistrigiceps*, hereafter the BRW), a rare host of the common cuckoo (*Cuculus canorus*, hereafter the cuckoo) for which information concerning its anti-parasitic defenses is lacking. The egg recognition experiment included testing of host egg recognition, the effect of UV reflectance, the significance of the sharp and blunt poles of the eggs, and the mechanism used for recognition. A nest intruder experiment tested the hosts' response toward the common cuckoo during both egg incubation and nestling stages. The BRW was sympatrically breeding with the oriental reed warbler (*A. orientalis*, hereafter the ORW) in our study area. However, although the breeding density of these two hosts is similar, the parasitism rate of BRW by the cuckoo is very low (0.42%), while this value in ORW is near half (49.9%) in comparison (Yang et al. 2017). Therefore, this study aims to provide an up-to-date picture of anti-parasitic defenses in the BRW that can help explain the mystery of its low rate of parasitism. We proposed four predictions: (1) The BRW should possess high rejection capacity toward the parasitic eggs based on its low parasitism rate. (2) The birds should use the true or template-based recognition mechanism since

multiple parasitism has not been observed. (3) The BRW should recognize eggs with manipulation on the blunt pole rather than on the sharp pole according to the blunt egg pole hypothesis. (4) The BRW should show stronger aggression to the common cuckoo than to harmless controls, but the aggression should be specific to the incubation stage rather than to the nestling stage, as the former stage is affected by cuckoo parasitism.

Materials and methods

Study area and nest sampling

This study was performed from May to August of 2014 in the reed habitat of Zhalong National Nature Reserve (46° 48−47° 31′ N, 123° 51−124° 37′ E), located north of the Songnen plain in Heilongjiang province, northeastern China (Wang et al. 2020a, b). The BRW is only distributed in some areas of South to Southeast Asia (Robson 2000; Round and Fisher 2009; Yong et al. 2015). Similar to the ORW, the BRW also build nests of similar structure in reed habitats, but its body size is smaller (Yang et al. 2016). Nests of the BRW were located in the reed habitats of the study area. To reduce the pseudo-replication risk of repetitive nest sampling for the experiment, we avoided sampling two nests within 200 m that were non-overlapping in a breeding cycle. A breeding cycle refers to the period between nest-building and nestlings being fledged. We assumed that two nests that overlapped in this period belonged to different parents. We measured the egg width and length using a Vernier caliper (precision of 0.01 mm), and calculated the egg volume by the formula of (Hoyt 1979) to represent the egg size. Eggs from different nests from the BRW, ORW, and cuckoo ($n = 12$ for each) were used as representatives for egg size calculation and the quantification of color and pattern.

Quantification of egg color and pattern

Egg color was measured by using a spectrophotometer (Avantes-2048; Avantes, Apeldoorn, the Netherlands) to obtain the reflectance. Six measured points were randomly selected on each egg, with three on the background color and three on the color of the markings, and the measurements were then averaged to represent the colors of background and markings. The reflectance data were analyzed using Goldsmith's tetrahedral color space (Goldsmith 1990), an advocated visual model for egg color analyses as processed by avian tetrachromatic visual systems (Stoddard and Prum 2008), where the average spectral sensitivity curves for UVS-type avian retinas were provided by Endler and Mielke (2005). Each spectrum is represented by a point in a tetrahedron in which the vertices correspond to exclusive

stimulation of the blue- (B), green- (G), red- (R), and UV-sensitive cones. Each color point is described by its spherical coordinates (θ, φ, r), where θ and φ represent the horizontal (RGB) and vertical (UV) components of a hue, respectively, and r is the length of the color vector and represents chroma (i.e., color saturation). The hue distributions were visualized independently of chroma by mapping colors onto a unit sphere centered on the achromatic origin using the Robinson projection, where θ $[-\pi; \pi]$ corresponds to longitude and $\varphi[-\pi/2; \pi/2]$ to latitude (Stoddard and Prum 2008). The normalized brilliance, a measure of achromatic brightness, was calculated following the method of Stoddard and Prum (2008). For the quantification of egg patterns, the normalized energies of seven spatial scales of egg maculation intensity were calculated using granularity analysis. The normalized energies of seven filter sizes (1, 2, 4, 8, 16, 32, and 64) from small to large refer to seven scales of egg maculation intensity from large to small (Stoddard and Stevens 2010).

Egg recognition experiment

To examine the egg recognition mechanism in the BRW host, five trials were performed. These were as follows: (1) A single parasitism trial ($n = 19$), in which one randomly selected host egg in the clutch was exchanged for one ORW egg. As the cuckoo egg mimics the ORW egg, we used the ORW egg (hereafter the parasitic egg) to represent the parasitic egg from the cuckoo. This trial aimed to test the egg recognition capacity of parasitic eggs by the host. (2) A multiple parasitism trial ($n = 14$), in which only one randomly selected host egg was left in the clutch while the other host eggs were exchanged for parasitic eggs (i.e., the natural clutch size was retained); this trial aimed to test the egg recognition mechanism of the host, where rejecting the one host egg means that the host uses a discordant recognition mechanism (recognition based on the discordance of egg number), while rejecting at least one parasitic egg indicates that the host uses a template recognition mechanism (recognition based on an instinctive or learned template). (3) A blunt pole trial ($n = 15$), in which one randomly selected egg was divided into two approximately equal-sized parts (the blunt and sharp poles) across their diagonal axis (Polačiková and Grim 2010), and then 40 black marking points with 1 mm diameter were evenly added to the blunt pole of that egg using a waterproof marker pen. (4) A sharp pole trial ($n = 15$), in which the procedure was as same as in the blunt pole trial except that the sharp pole was painted; these two trials aimed to investigate which pole held the cues for foreign egg recognition in the host. (5) A controlled trial ($n = 12$), in which the host clutch was touched and visited as frequently as in the above trials. This was conducted to control for the effect of manipulation. The manipulation of all these trials was performed during the early incubation

stage of the host nest (i.e., the first 3 days of incubation after clutch completion) and checked for 6 days (first, third, and sixth day) after manipulation to confirm the reaction from the host. The reaction was classified as acceptance or rejection. Acceptance refers to the result that the host clutch was continuously incubated for 6 days without any egg rejection by the host, while rejection refers to the manipulated egg being ejected, buried, or deserted by the host within 6 days. No ejection or desertion was found in the control trial.

Intruder recognition experiment

To investigate the reaction toward nest intruders by the host, taxidermist dummies of the cuckoo (the brood parasite), sparrowhawk (*Accipiter nisus*, the predator), or oriental turtle dove (*Streptopelia orientalis*, the harmless control) were mounted at a distance of 0.5 m from and pointed toward the host nest during incubation ($n = 28$) or nestling stage ($n = 19$). The reaction by the host was recorded during 15 min of observation and ranked as a score of 1 for no reaction, 2 for producing alarm calls, 3 for mobbing the dummy, or 4 for attacking the dummy, thus rating the host aggression behavior from weak to strong. The dummies were presented at intervals of 1 h in a random order to avoid the effect of presentation order, and two replicates of each dummy type were randomly selected to avoid pseudo-replication. No significant differences were found in reaction toward the two dummy replicates (incubation stage: $Z = 0.653$, $P = 0.514$; nestling stage: $Z = -0.243$, $P = 0.808$, Cumulative Link Mixed Model [CLMM]), and thus we pooled the data for subsequent analyses.

Statistical analyses

Analysis of variance (ANOVA) and the calculation of least significant difference (LSD) was used for egg size comparison among BRW, ORW, and cuckoo, while Student's t test was used for comparison of egg color and pattern between the cuckoo and the BRW or ORW. A generalized linear mixed model (GLMM) with binomial distribution was used to analyze the results of the egg recognition experiment in which the response variable was the host reaction (acceptance/rejection). The treatment (manipulation of different trials), egg-laying date, and clutch size were fixed effects, while the nest identity was a random effect. The analyses involved two models. The first model compared the host reaction between the single parasitism trial and multiple parasitism trial; the second model compared the blunt pole trial and the sharp pole trial. CLMM was used to deal with the ranked variable the of intruder recognition experiment. Three models were involved. Model 1 tested the difference in aggression between the dummies in the incubation stage, with the nest identity, egg-laying date, and clutch size as

random effects; model 2 tested the difference in aggression between the dummies during the nestling stage, with the nest identity, egg-laying date, and brood size as random effects; and model 3 tested the difference in aggression between incubation and nestling stages and the interaction between dummies and stages, with the nest identity and egg-laying date as random effects. Because not all host nests in the incubation stage lasted until the nestling stage, model 3 only included the data of nests that possessed both incubation and nestling stages. ANOVA, LSD, and Student's *t* test were run by SPSS 25.0 for Windows (International Business Machines Corporation, New York, USA), while GLMM and CLMM were run by the *nlme* and *ordinal* packages, respectively, in R (Version 4.1.0) for Windows (https://www.r-project.org/). The Robinson projection of egg characteristics was generated using Matlab 2012a for Windows (MathWork Inc.). Values were presented as mean ± SE, and the significance level was set to $P = 0.05$.

Results

The egg size was significantly different between the BRW, ORW, and cuckoo ($F = 296.204$, df = 2, $P < 0.001$, ANOVA), with the largest size being in the cuckoo (3.09 ± 0.72 cm^2, $n = 12$), the median in the ORW (2.79 ± 0.44 cm^2, $n = 12$), and the smallest in the host BRW (1.35 ± 0.40 cm^2, $n = 12$). All post hoc comparisons between two species were significant ($P < 0.001$ for all comparisons, LSD). The RGB component of hue in egg background color did not differ between the cuckoo and ORW eggs ($t = 1.657$, df = 22, $P = 0.120$, Student's t test) or BRW eggs ($t = -0.228$, df = 22, $P = 0.822$, Student's *t* test; Fig. 1A). However, the UV component of hue in egg background color was inconsistent between these two aspects (cuckoo vs ORW: $t = -3.294$, df = 22, $P = 0.003$; cuckoo vs BRW: $t = 0.745$, df = 22, $P = 0.464$, Student's *t* test). For the egg markings, cuckoo eggs did not differ from ORW eggs in either the RGB ($t = 0.045$, df = 22, $P = 0.965$, Student's *t* test; Fig. 1A) or UV ($t = 0.143$, df = 22, $P = 0.888$, Student's *t* test) components, but differed from BRW eggs in both aspects (RGB: t = 5.871, df = 22, $P < 0.001$; UV: $t = -3.162$, df = 22, $P = 0.005$, Student's *t* test; Fig. 1A). The chroma of the egg background color in cuckoo eggs differed from both ORW and BRW eggs, while the chroma of egg markings did not show significant differences to either (Fig. 1B). For the normalized brilliance, the cuckoo eggs were significantly different from the BRW eggs in both the background color and markings, but not from the ORW eggs (Fig. 1C). For the normalized energies of egg pattern, these were different between cuckoo and ORW eggs in the small and large filter sizes but similar in median filter sizes. In contrast, the same comparisons between cuckoo and BRW showed opposite results (Fig. 1D). In summary, the results

indicated that cuckoo eggs were mimetic to ORW eggs in many aspects, but differed from BRW eggs in ways visible to both bird and human eyes.

For the egg recognition experiment, the host rejected 100% of parasitic eggs in the single parasitism trial ($n = 19$) and multiple parasitism trial ($n = 14$). Furthermore, 80% of the manipulated eggs in the blunt pole trial were rejected ($n = 15$), while no rejection was found in the sharp pole trial ($n = 15$). All rejection was performed by ejection without rejection error. The results of the GLMM analysis indicated that neither the treatment nor the other effects predicted the egg recognition of single parasitism vs multiple parasitism trials (Table 1). Furthermore, the treatment predicted the egg recognition of blunt pole vs sharp pole trials (Table 1). For the nest intruder experiment, model 1 for the incubation stage found that hosts' aggression toward the cuckoo (score: 3.14 ± 0.16) was significantly higher than toward the dove (score: 2.36 ± 0.24), but the effect did not reach statistical significance between the cuckoo and the sparrowhawk (score: 2.64 ± 0.16) (Table 2). However, model 2 for the nestling stage did not find a significant difference in aggression toward the cuckoo, dove, or sparrowhawk. Model 3, which combined both stages, also presented similar results, except that the increased aggression toward the cuckoo and sparrowhawk reached a level of statistical significance (Table 2). These results indicate that the host mobbed and attacked cuckoo more frequently than other nest intruders.

Discussion

This study demonstrated that the BRW hosts rejected 100% of parasitic eggs, a result that was consistent with our first prediction that the BRW possesses a high recognition capacity to distinguish parasitic eggs from their own eggs. Such a strong rejection would explain why the BRW is hardly parasitized by the cuckoo. The host also rejected 100% of parasitic eggs in the multiple parasitism trial, which agrees with our third prediction that the host used a true or template-based mechanism of egg recognition. Because the parasitism rate was very low in the BRW, multi-parasitism was impossible, and thus template-based recognition was reasonably thought to be an adaptive mechanism. Most previous studies have also supported the hypothesis that hosts only use a template-based mechanism for egg recognition (Peer and Sealy 2001; Lyon 2007; Bán et al. 2013; Lang et al. 2014; Tosi-Germán et al. 2020; Yi et al. 2020; Ma and Liang 2021), while few studies have found that the discordance mechanism was involved to some extent (Moskát et al. 2010; Yang et al. 2014). However, no host species were found to use the mechanism of discordance as the only rule for egg recognition. The discordance mechanism should be a relatively simple
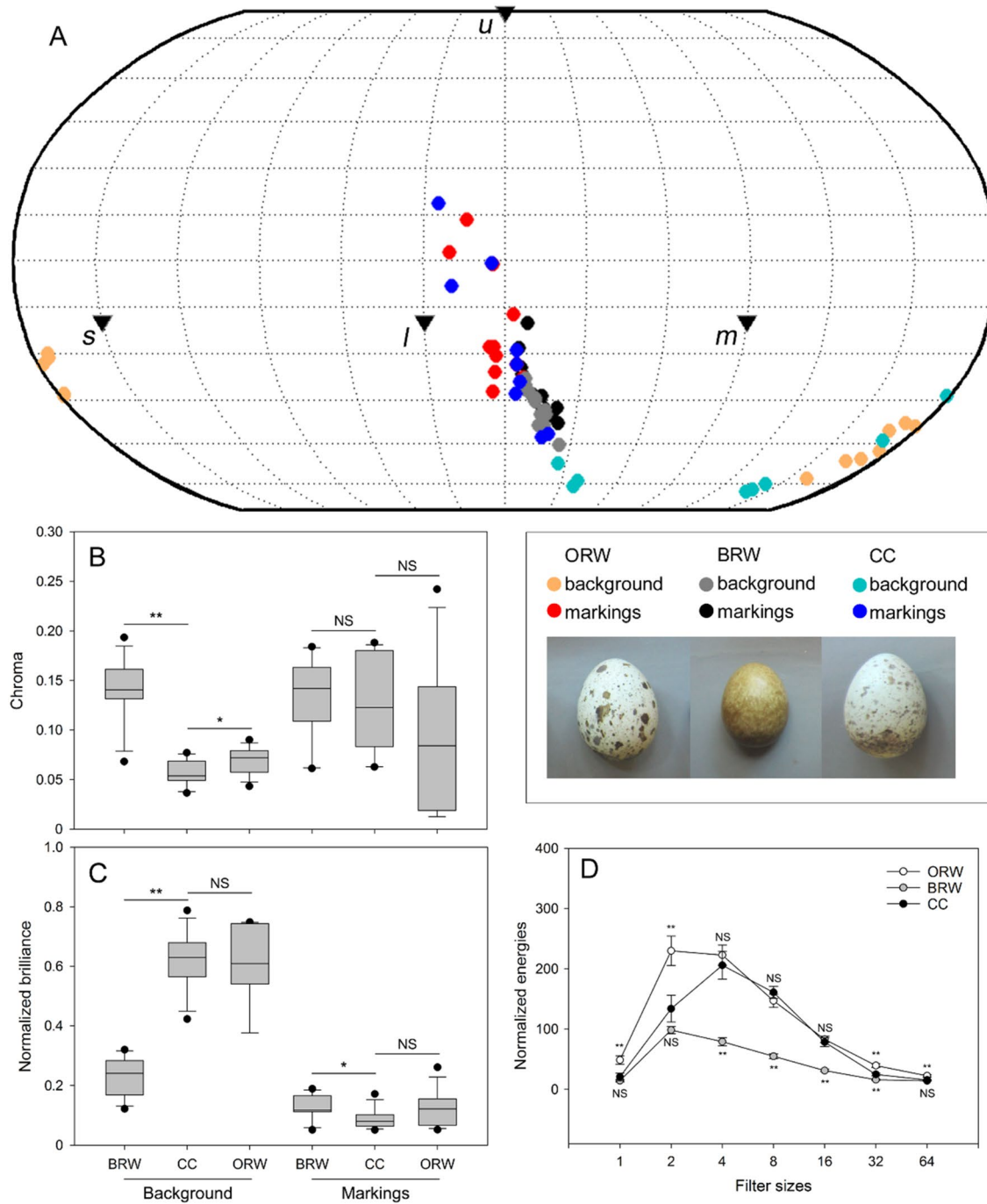
Fig. 1 Robinson projection of egg color hue (**A**), chroma (**B**), and normalized brilliance (**C**) for background and marking colors (box-plots refer to the median, 10th, 25th, 75th, and 90th percentiles) in the oriental reed warbler (ORW), black-browed reed warbler (BRW), and common cuckoo (CC), and comparison of egg pattern by granularity method of recognition (Rensch 1925; Moskát et al. 2009). However, the recognition error rates of the discordance mechanism were varied, especially when a host was confronted with multiple parasitism or when laying heterogeneous clutches (Moskát et al. 2010, 2014).

analysis (**D**) (error bars refer to mean and SE). $P > 0.05^{NS}$; $P < 0.05*$; $P < 0.01**$. Labels beside the lines of ORW and BRW refer to the significance levels of comparisons with CC. Sample sizes were 12 for each species

Furthermore, our results indicated that the host rejected 80% of eggs with manipulation of the blunt pole, but eggs with the counterpart manipulations on the sharp pole were accepted. Such a significant difference between the blunt and sharp poles indicated that the blunt pole was playing an

Table 1 The results of generalized linear mixed model analysis for the egg recognition experiment in the black-browed reed warbler

Models	F	df1	df2	P
Single parasitism vs multiple parasitism				
Intercept	1.802×10^{33}	1	29	< 0.001***
Treatment	1.000	1	29	0.388
Egg-laying date	3.000	1	29	0.087
Clutch size	< 0.001	1	29	0.486
Blunt pole vs sharp pole				
Intercept	56.107	1	26	< 0.001***
Treatment	56.107	1	26	< 0.001***
Egg-laying date	0.003	1	26	0.057
Clutch size	2.050	1	26	0.164

$P < 0.05$*; $P < 0.01$**; $P < 0.001$***

important role in providing cues for egg recognition. This result, therefore, supported the blunt egg pole hypothesis (Polačiková et al. 2007, 2010; Polačiková and Grim 2010).

Finally, our last prediction was mostly supported: the host showed aggressive behavior towards cuckoos in the incubation stage, and this behavior was stronger than that toward the harmless control. This indicated that the host was capable of recognizing the cuckoo as a parasite, as opposed to as a harmless intruder. The host mobbed and attacked cuckoos more frequently than doves or sparrowhawks because the former was harmless, while the latter presented a danger to host adults. More importantly, the aggression toward the cuckoo was reduced to a non-significant level during the nestling stage, further supporting our prediction and the dynamic risk assessment hypothesis (Kleindorfer et al. 2005), since the host adjusted its aggression toward the cuckoo as a response to parasitism risk (i.e., parasitism risk occurs in the incubation stage but not in the nestling stage), implying that the aggression toward the cuckoo was a specific response to brood parasitism. Previous studies have generally used this as a necessary criterion for evaluating a species of bird to be a host utilized by cuckoos (Sealy et al. 1998; Feeney et al. 2012). This result, therefore, not only indicated that the BRW was effective in nest defense against the cuckoo but also implied that it was utilized against other *Cuculus* species. One possible explanation for the near absence of cuckoo parasitism in the BRW may be that it was a former host with historical interaction with the common cuckoo, while the ORW is a more recent host. An alternative explanation is that the BRW was utilized by another host race of the common cuckoo or other *Cuculus* species, but in this study area, such host races or *Cuculus* cuckoos were absent.

To summarize, this study provided new information concerning anti-parasitic defenses in the BRW. The strong capacity of egg recognition combined with the high and specific aggression toward cuckoo in this host species may together help to explain why it was hardly parasitized in this study area. Although parasitism was nearly absent, the host maintained such anti-parasitic defenses at a high level, implying that historical interaction with the common cuckoo or dispersal from populations that were parasitized by another race of the common cuckoo or other *Cuculus* species. Alternatively, it is possible that the arms race between BRW and common cuckoo has already been terminated, and the rare parasitism is due to a random host choice by the cuckoo.

Table 2 The results of the cumulative link mixed model for the intruder recognition experiment in the black-browed reed warbler

Reference variable	Compared variable	Estimate	S.E	Z	P
Model 1: Incubation stage					
Cuckoo	Dove	−0.945	0.304	−3.112	0.002**
	Sparrowhawk	−0.507	0.296	−1.715	0.086
Model 2: Nestling stage					
Cuckoo	Dove	−0.695	0.356	−1.953	0.051
	Sparrowhawk	−0.069	0.349	−0.198	0.843
Model 3: Incubation stage vs Nestling stage					
Incubation stage	Nestling stage	−0.612	0.368	−1.665	0.096
Incubation stage × Cuckoo	Incubation stage × Dove	−1.517	0.385	−3.938	< 0.001***
	Incubation stage × Sparrowhawk	−0.777	0.363	−2.138	0.033*
	Nestling stage × Dove	−0.683	0.368	−1.860	0.063
	Nestling stage × Sparrowhawk	−0.076	0.355	−0.215	0.830

$P < 0.05$*; $P < 0.01$**; $P < 0.001$***

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

Ethical standards The experiments comply with the current laws of China, where they were performed. Fieldwork was carried out under the permission of Zhalong National Nature Reserve.

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