OXFORD

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Coevolution between Himalayan cuckoos and 2 sympatric Pycnonotidae hosts

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Handling editor: David Swanson

Abstract

Selection due to cuckoo parasitism is responsible for the evolution of anti-parasitism defenses in hosts. Different host species breeding sympatrically with a single parasitic cuckoo may evolve different strategies to reduce the risk of counter cuckoo parasitism, resulting in different interactions between cuckoos and hosts in areas of sympatry. Here, we studied the coevolutionary interactions between Himalayan cuckoos *Cuculus saturatus* and 2 sympatric and closely related potential hosts belonging to the family Pycnonotidae, the brown-breasted bulbul *Pycnonotus xanthorrhous* and the collared finchbill *Spizixos semitorques*. We investigated parasitism rates and nest-site selection (nest height, nest cover, human disturbance, perch height, forest distance, and degree of concealment) related to parasitism risk, nest defense against a cuckoo dummy, and egg rejection against cuckoo model eggs. Bulbuls used specific nest sites that were further away from forests than those of finchbills, and they behaved more aggressively toward cuckoos than finchbills. In contrast, bulbuls possessed moderate egg rejection ability, whereas the finchbill rejected 100% of cuckoo model eggs. We suggest that selection of a nest site away from forests by the bulbul explains the absence of parasitism by Himalayan cuckoos. We suggest that these interspecific differences in nest-site selection and nest defense indicate alternative responses to selection due to cuckoos.

Key words: *Cuculus saturatus*, distance to forest, parasitism risk, *Pycnonotus xanthorrhous*, *Spizixos semitorques*.

Whereas most bird species build nests for incubating their eggs and rearing their offspring, some species never build nests, but rather lay eggs in the nests of other birds; these special taxa are called obligate avian brood parasites (Davies 2011). Brood parasitism is costly for hosts, because they bear the parental care transferred from the genetically unrelated parasites (Yang et al. 2019). Coevolutionary interactions between parasites and their hosts is a textbook example of an arms race in which parasites have evolved a variety of mechanisms that are subsequently fine-tuned to exploit their hosts, and

hosts have, in turn, developed strategies of defense against parasitism (Rothstein 1990; Soler 2014).

Several hypotheses have been proposed to explain how hosts defend themselves against brood parasites. Among the anti-parasitic defenses, frontline defenses refer to anti-parasitic defenses of hosts prior to parasitism (Feeney et al. 2012), and the refuge hypothesis suggests that the hosts may build nests close to human settlements (Møller 2010; Liang et al. 2013) or in open areas (Øien et al. 1996; Moskát and Honza 2000) because parasites keep a safe distance

from humans, and open areas provide fewer perches for cuckoos to monitor the reproductive behavior of hosts. Open areas may also increase predation rate by birds of prey (Chace and Walsh 2004) and hence increase the predation risk for cuckoos.

Moreover, recently 2 alternative hypotheses have put forward to explain the intensity of different lines of defense in cuckoo hosts. The strategy-blocking hypothesis suggests that success at 1 stage of defense may reduce selection for defenses at another stage (Planqué et al. 2002; Britton et al. 2007). For example, magpie *Pica pica* hosts that rejected parasite eggs showed lower levels of nest defense against parasites (Soler et al. 1999). Alternatively, the strategy facilitation hypothesis suggests that one line of defense may facilitate the evolution of another (Kilner and Langmore 2011). For example, prinia *Prinia flaviventris* populations that attacked parasites rejected parasite eggs more frequently and quickly than populations that did not attack parasites (Yang et al. 2014a).

The brown-breasted bulbul (*Pycnonotus xanthorrhous*, hereafter the bulbuls) and the collared finchbill (*Spizixos semitorques*, hereafter the finchbills) are 2 closely related, sympatric species from the bulbul family Pycnonotidae that build similar nests, lay similar-looking eggs, and breed in sympatric areas. According to our observations, in our study site, the finchbills were parasitized by Himalayan cuckoos (*Cuculus saturatus*, hereafter the cuckoos) with a parasitism rate of 2.3% (5 parasitized nests out of 216 host nests), whereas no parasitism was found in the bulbuls ($n = 158$). Furthermore, according to the cuckoo host list summarized by Lowther (2014), the finchbill was recorded as a host of the Sunda lesser cuckoo *Cuculus lepidus*, whereas no form of parasitism was found in the bulbul. These data suggested that the finchbill was a causal host and the bulbul was a potential host of cuckoos. This, therefore, provided an ideal opportunity to study parasitism selection on these 2 potential host species by cuckoos. The anti-parasite behaviors of these 2 host species have not been examined previously except for our studies in this area. To understand the interactions between these 2 closely related host species and the Himalayan cuckoo, we investigated their parasitism rates, nest-site characteristics, nest defense behavior, and egg discrimination ability. By comparing these parameters between the 2 host potential species, we aimed to reveal the possible reasons for differences in host use by cuckoos. We predicted that the bulbuls were not utilized by cuckoos probably (1) because they chose nest sites that help reduce parasitism or (2) because they have evolved highly effective anti-parasite defenses, which could support either the strategy-blocking or strategy facilitation hypotheses, depending upon which types of anti-parasite defense they possess.

Materials and Methods

Study area and study species

This study was performed in Kuankuoshui (KSS) National Nature Reserve (28°10' N, 107°10' E) during 2008–2013 and in Baihuahu (BHH; 26°40'N, 106°31' E) during 2012–2013. Both study sites are located in Guizhou Province, Southwest China, separated by ca. 200 km. The KSS Nature Reserve is situated in a subtropical moist broadleaf mixed forest interspersed with abandoned tea plantations, shrubby areas, and open fields used as cattle pastures (Yang et al. 2010, 2013). BHH is an island park in the suburban area of Guiyang City (Su et al. 2016). Several cuckoo species are found in both study areas, including the large hawk cuckoo *Hierococcyx sparverioides*, the common cuckoo *Cuculus canorus*, the Himalayan cuckoo, and the lesser cuckoo *Cuculus poliocephalus*. However, according to our

observations, the Himalayan cuckoo was found to be nearly exclusively restricted to forests, whereas the common cuckoo and lesser cuckoo were nearly always found in open areas. Large hawk cuckoos were found in both forests and open areas. None of these cuckoo species were found to use the bulbuls, whereas only the Himalayan cuckoos were found to parasitize the finchbills with non-mimetic white eggs with few and fine markings of a dark red color (Figure 1).

The brown-breasted bulbul and collared finchbill belong to the same bulbul family (Pycnonotidae) but are in different genera, and both have similar geographic ranges (Zheng 2017). The bulbuls and finchbills both build open cup-shaped nests in shrubs from forest to open areas at heights of 0.94 ± 0.05 m ($n = 121$) and 1.14 ± 0.04 m ($n = 144$), respectively. Both species lay violet-colored, densely marked eggs with clutch sizes of 3.10 ± 0.69 ($n = 78$) and 2.62 ± 0.53 ($n = 95$), respectively (Figure 1). According to the host nests, we found and our observations, the population density of bulbuls was larger than that of finchbills.

Comparison of nest-site characteristics

Nest-site characteristics of bulbuls and finchbills were only measured in KKS. Nests of bulbuls and finchbills were found by monitoring the respective reproductive behavior of any observed individual and systematically searching all potential nest sites. Six important parameters of nest sites that may affect the risk of parasitism were measured as (1) nest height, measured as the height from ground to nest rim using a tape measure to the nearest centimeter; (2) nest cover, measured as the percentage of nest concealment by leaves and branches (unit: %) when the nest was viewed from 50 cm above by using a mirror; (3) human disturbance (unit: m), measured as the distance to a road (unit: m) with regular human presence (i.e., roads that connect different villages); (4) perch height (unit: m), measured as the distance from the nearest perch (but not the same shrub as the host nest) that could facilitate monitoring of the host by the cuckoo (i.e., the distance from the top of a perch site to the host nest) using a laser range finder (Victory 10×56 T RF, Carl Zeiss Inc., Jena, Germany); (5) forest distance (unit: m), measured by a laser range finder as the distance from the nest to the nearest forest as a measure of the probability of encountering a Himalayan cuckoo (for nests in forests, the value was set to 0); and (6) the degree of concealment of host nests was quantified by the number of directions that had a view of the nest (0 represents no nest view, whereas 4 represents all 4 directions with a nest view; Moskát and Honza 2000).

Parasitism experiments

Naturally parasitized nests were identified by parasite eggs or nestlings, and these nests were not used in the parasitism experiment. The parasitism experiments were conducted in both KKS and BHH for both potential host species. The Himalayan cuckoo lays nearly immaculate white eggs, and thus white model cuckoo eggs made of polymer clay with a standard size of 21.5 mm in length and 15.4 mm in width and a standard mass of 2.2 g (similar to that of the Himalayan cuckoo) were inserted into the nests of bulbuls and finchbills to investigate their responses. We used immaculate white model eggs rather than white model eggs with markings because cuckoo eggs only have very sparse patterning (Figure 1), and immaculate model eggs are much easier to standardize. Because host nests were distributed across large areas, and because we attempted to keep disturbance as low as possible, we monitored active nests every 2–3 days before the parasitism experiments. During the experiments, nests were artificially parasitized during the early incubation

Figure 1. Nests and eggs of the brown-breasted bulbul (**A**) and the collared finchbill (**B**) with a Himalayan cuckoo egg in the bottom right corner of (**B**). Photographs by Bruce Lyon (birds) and Canchao Yang (nests and eggs).

period (in the first 3 days of incubation) and then monitored for 6 days on a daily basis ($n = 23$ for finchbills and $n = 89$ for bulbuls). Responses by hosts were classified as acceptance, if foreign eggs were incubated or kept warm, or rejection, if foreign eggs were ejected after 6 days of monitoring. The 2 host species are sufficiently large to grasp the model eggs, and no rejection cost or trace of pecking was found in this study. Some nests were visited by the same procedure without parasitism manipulation as a control for disturbance, and no desertion was detected in this group for either bulbuls ($n = 25$) or finchbills ($n = 20$). Nest-site characteristics were not measured in the control group.

Cuckoo dummy experiments

Cuckoo dummy experiments were conducted in both KKS and BHH for the bulbuls, but only in KKS for finchbills because the number of nests in BHH was insufficient for dummy experiments. For each host nest, a stuffed dummy of a Himalayan cuckoo, besra *Accipiter virgatus*, or Oriental turtle dove *Streptopelia orientalis* was mounted pointed toward the nest at a distance of 0.5 m. The predatory sympatric besra and the benign Oriental turtle dove were selected as predatory controls and species that pose no threat, respectively. The plumage of the besra is similar to that of the cuckoo in possessing bars on the belly. However, the besra is harmful to adult hosts, whereas the cuckoo is not. The responses of hosts were predicted to be aggressive against a cuckoo dummy with contact, aggressive toward the besra dummy without contact, and not aggressive toward the dove dummy. The time

interval between presentations of 2 dummies was 1 h, and we adopted a random sequence of model presentations to avoid any effects of sequence. Two dummy individuals were chosen randomly for each model to avoid pseudoreplication (Moskát 2005), although our tests showed that there were no significant effects of dummy identity on responses. After the dummy was mounted, we waited for the hosts to appear, and 5 min of observation for the responses of focal birds was conducted when the birds arrived at the nest within 15 min. The sex of focal birds was not recorded because it could not be identified by eye. The strength of responses by hosts (from strong to weak) was recorded and scored as (1) attack (score 4: physical contact with the dummy by hosts); (2) mobbing (score 3: flying close to the dummy to feign attack without physical contact); (3) alarm (score 2: producing alarm calls); and (4) no aggression (score 1). The observer (T.S.) was hidden ca. 5 m away in the bushes to record the hosts' responses. The experiment was terminated if hosts directly attacked the dummies, or if hosts did not appear within 15 min. We did not use a blinded method because it is impossible to apply such a method in this study, and the behavioral responses by hosts were obviously distinctive and not affected by subjective human evaluation. Moreover, parasitism experiments and cuckoo dummy experiments were not performed in the same nests.

Statistical analyses

Discriminant analysis was used to assess whether the nest-site characteristics could be partitioned between bulbuls and finchbills. We used a binomial stepwise logistic regression model to analyze the

Table 1. Classification function coefficients of nest-site characteristics between brown-breasted bulbul and collared finchbill at KKS nature reserve by discriminant analysis

Parameters	Brown-breasted bulbul	Collared finchbill
Nest height[a]	3.070	4.004
Human disturbance[b]	0.055	0.036
Forest distance[c]	0.034	0.008
Constant	−3.517	−3.092

[a] Height of the nest from the ground; [b] percentage of nest concealment by leaves and branches when the nest was viewed from 50 cm above; [b] distance to a road with regular presence of local people; and [c] distance from the nest to a forest.
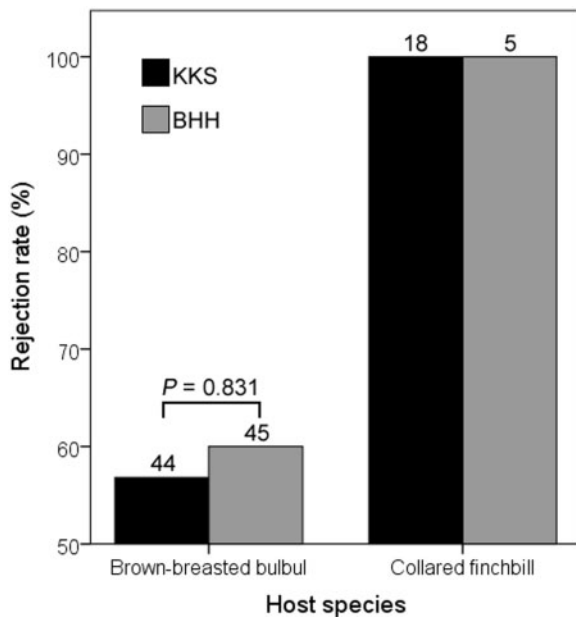

Figure 2. Results of the parasitism experiment on bulbuls and finchbills in KKS and BHH nature reserves, respectively.

effects of clutch size, location (KKS and BHH), and species (bulbuls and finchbills) on egg rejection (response variable, acceptance = 0 and rejection = 1) based on the preference for lowest AIC/BIC values. For the dummy experiment, we used cumulative link mixed models (CLMMs) for analyses because the aggressive behaviors were ordinal-dependent variables. Four separate models were run, including the bulbul-only model, the finchbill-only model, the combined model (combing the bulbul and finchbill data), and the cuckoo-only model (only the cuckoo dummy data were considered). For all models, the scores of responses toward the dummy were dependent variables; the nest ID was a random effect, and the dummy used in the experiment was a fixed effect. The interaction between dummy and dummy order was also tested. For the bulbul-only model, location was also included as a fixed effect, whereas for the combined model the interaction between dummy and host species was tested. Post hoc pairwise comparisons were used for significant effects. Analyses of the data on nest-site characteristics and parasitism experiment were performed in IBM SPSS 20.0 for Windows (IBM, Inc., Armonk, NY), whereas the dummy experimental data were analyzed using the CLMMs function in the R package ordinal (version 4.13-0). Values were presented as means ± SE, and the significance level was set to $P < 0.05$.
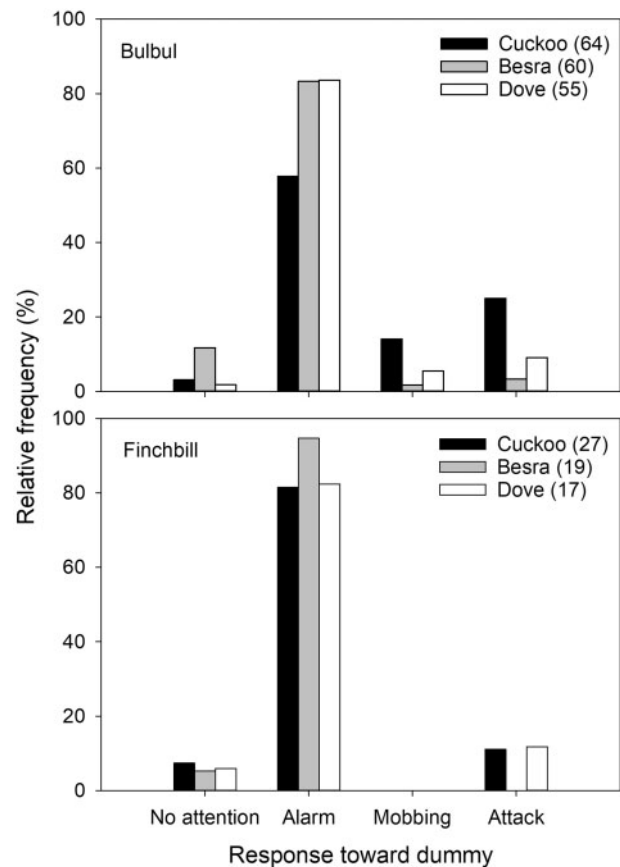

Figure 3. The frequencies of different responses toward dummy species in KKS Nature Reserve, southwestern China, with sample sizes in brackets. Post hoc comparisons showed that the aggression in bulbuls was significantly stronger to the cuckoo than to besra/dove (but did not differ between the besra and the dove).

Results

Nest-site characteristics and egg rejection

According to the discriminant analysis, the nest characteristics between bulbuls and finchbills were classified by the nest height, human disturbance, and forest distance with 76.2% of original grouped cases correctly classified (chi-square = 52.799, $df = 3$, $P < 0.001$, Wilks' Lambda test of function). The bulbuls built lower nests with longer distances to roads and forest than the finchbills (Table 1). Both the bulbuls and finchbills showed egg rejection toward foreign eggs by ejection. Whereas the bulbul rejected 56.6% ($n = 89$) of non-mimetic foreign eggs, the finchbill rejected 100% ($n = 15$) (Figure 2). Logistic regression analyses indicated that only the species (bulbuls or finchbills) predicted the egg rejection behavior (species: Wald = 7.404, $df = 1$, $P = 0.007$; clutch size: Wald = 1.327, $df = 1$, $P = 0.249$; location: Wald = 1.170, $df = 1$, $P = 0.279$).

Aggression toward the parasite

In the dummy experiment, the bulbuls attacked 25% and mobbed 14.1% of cuckoos ($n = 64$), whereas comparable values were 11.1% and 0% for the finchbill ($n = 27$), respectively (Figure 3). The bulbul-only CLMM indicated that bulbuls responded differently toward different dummies ($Z = −2.751$, $P = 0.006$). Post hoc comparisons showed that the bulbuls were more aggressive toward cuckoo

Table 2. Statistical analyses of dummy experiments by CLMMs

Models	Source	Z	P-value
The bulbul-only	Dummy	−2.751	0.006[**]
CLMM	Location	0.622	0.534
	Dummy × dummy order	1.418	0.156
The finchbill-only	Dummy	0.230	0.818
CLMM	Dummy × dummy order	−0.373	0.709
Combined CLMM for	Dummy	6.774	0.010[*]
2 host species	Dummy × species	−2.442	0.015[*]
	Dummy × dummy order	−0.528	0.597
The cuckoo-only	Host species	−2.457	0.014[*]
CLMM	Dummy order	1.516	0.129

[*]$P < 0.05$, [**]$P < 0.01$.

than besra/dove dummies ($P < 0.05$ for both) but not between besra and dove dummies ($P > 0.05$). Effects of location and interaction between dummy and dummy presentation order were not significant for the bulbuls (Figure 3; Table 2). However, the finchbill-only CLMM showed that finchbills exhibited low aggression (mainly by alarm) toward different dummies without significant differences (Figure 3; Table 2; $Z = 0.230$, $P = 0.818$). Consistent with this, the combined CLMM for 2 host species indicated that the responses toward dummies differed significantly among dummies ($Z = 6.772$, $P = 0.010$), and such responses to dummies changed with the host species ($Z = 2.442$, $P = 0.015$). Moreover, when only cuckoo dummies were considered there was a significant difference in responses toward cuckoo dummies between the 2 host species (Figure 3; Tables 2; $Z = −2.457$, $P = 0.014$).

Discussion

According to our findings, the bulbuls built nests further away from the forests compared with finchbills. This result seems to support our prediction concerning the refuge hypothesis. The nest characteristics of bulbuls may be a specific adaptation to prevent them from being parasitized by the Himalayan cuckoo, because the cuckoos were almost exclusively found in forests. Previous studies have shown that hosts can avoid brood parasitism by breeding indoors (Liang et al. 2013) or can reduce the risk of parasitism by selecting nest sites far from perches used by cuckoos (Øien et al. 1996; Moskát and Honza 2000). In other words, suitable host species for brood parasites may seek refuge in the proximity of humans to avoid parasitism (Møller et al. 2016) or may choose to build nests in sites far away from cuckoos to reduce the risk of parasitism, hence using refuges to avoid parasitism. However, alternatively such nest-site selection may be a result of niche differentiation (Armstrong and McGehee 1980), thereby providing a pre-adaptation for avoidance of cuckoo parasitism. Finally, it is worth mentioning that the opposite situation was found in brown-headed cowbirds (*Molothrus ater*) that were found to parasitize hosts nesting in forest interiors less frequently, because cowbirds prefer open habitats (Banks and Martin 2001).

Although nest height differed between bulbuls and finchbills, we assume that a difference of only 0.2 m (Table 1) would not change the risk of parasitism. In previous studies, nest height was found to correlate with parasitism rate by cowbirds (*Molothrus* spp.) (Smith 1981; Fleischer 1986; Banks and Martin 2001, but see Wiens 1963; Hackemack et al. 2016). Lower nests tended to suffer higher rates of parasitism, perhaps as a consequence of the cowbird's habit of searching for host nests close to the ground. However, cuckoos monitor hosts from a high perch, and thus a mere 0.2 m difference in nest height in our study should not affect parasitism risk. Furthermore, previous studies of cuckoos showed that nest height was not an important predictor of cuckoo parasitism (Moskát and Honza 2000; Jelínek et al. 2014).

Our results also indicated that the bulbuls were more aggressive toward Himalayan cuckoos (they attacked and mobbed cuckoos at higher frequency) but possessed weaker capacity for egg discrimination (rejected model eggs at lower frequency) than the finchbills. This result, therefore, may support the strategy-blocking hypothesis, because for the bulbuls the higher level of frontline defense toward parasites was accompanied by the lower level of egg rejection, whereas for the finchbills the situation concerning these 2 stages of defense was just the opposite. This is consistent with previous findings that success at early stages of defense may reduce selection for defenses at later stages, thus blocking the evolution of another costly defense that would be adaptive in its absence (Planqué et al. 2002; Britton et al. 2007). Moreover, the low level of response toward the besra dummy by both bulbuls and finchbills may have been due to few interactions with besras, or simply due to low density of besras.

Finally, it is possible that the Himalayan cuckoo also utilizes hosts in the deep forest, but the forest was characterized by tall trees that limited our nest search ability. The Himalayan cuckoo was the only parasite found to parasitize the finchbills, whereas the bulbul was not parasitized by any cuckoo species. Given that the investigation of parasitism rate was conducted for several years, it is unlikely that we missed parasitism by other cuckoo species. Furthermore, although the parasitism rate of the finchbill was low (2.3%), this does not imply that the finchbill is a non-preferred host of the Himalayan cuckoo. Our previous work has shown that in this study site the common cuckoo and ashy-throated parrotbill *Sinosuthora alphonsiana* have reached an advanced stage of coevolutionary interaction, with both parasite and host having evolved polymorphic eggs, even when the parasitism rate is low (4.3%, $n = 555$; Yang et al. 2010, 2014b). Moreover, the parasitism rate of finchbill may be underestimated because of the efficient egg rejection by the finchbill before our detection. In addition, the Himalayan cuckoo parasitizes Blyth's leaf warbler *Phylloscopus reguloides* in forest edges, although the sample size on which this is based was small (25%, $n = 4$). Although the bulbul was not parasitized, we assumed that the bulbul is a potential host for the Himalayan cuckoo rather than other cuckoo species because (1) the closely related finchbill was used by Himalayan cuckoos and (2) different cuckoo species or host races specialize on

parasitizing different or closely related hosts. For example, the common cuckoo host race that parasitizes ashy-throated parrotbills also exploits vinous-throated parrotbills, and these 2 host species lay eggs with similar appearance (Yang et al. 2015).

In summary, the contrasting differences in nest-site selection, intensity of aggression toward parasites, and egg rejection between the bulbuls and finchbills may provide evidence to support the strategy-blocking hypothesis. Finally, we suggest that future work, such as nestling recognition, is needed to be done to better understand this coevolutionary system.

Authors' Contributions

C.Y. and W.L. conceived the idea and designed the research. C.Y. and T.S. conducted the field sampling. C.Y. and Q.L. analyzed the data and wrote the draft manuscript. W.L. and A.P.M. improved the manuscript. All authors have read and approved the final manuscript.

Competing Interests Statement

The authors declare that they have no conflicts of interest.

Ethical Approval Statement

This article does not contain any studies with human participants performed by any of the authors. The experiments comply with the current laws of China where they were performed. Experimental procedures were in agreement with the Animal Research Ethics Committee of Hainan Provincial Education Centre for Ecology and Environment, Hainan Normal University (permit no. HNECEE-2016-003).

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