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Potential cuckoo hosts have similar egg rejection rates to parasitized host species

Tingting Yi[1,2], Yue-Hua Sun[2*] and Wei Liang[1*]

Abstract

Background: Thrush species are rarely parasitized by cuckoos, but many have a strong egg recognition ability. To date, there is a limited understanding of the relationship between host egg rejection and cuckoo parasitism rate.

Methods: By using egg experiments in the field, we compared egg rejection between two non-parasitized potential host species and two parasitized hosts of cuckoos in the same region.

Results: The White-bellied Redstart (*Luscinia phoenicuroides*), a host of the Common Cuckoo (*Cuculus canorus*), rejected 66.6% of blue model eggs; the Elliot's Laughingthrush (*Trochalopteron elliotii*), a host of the Large Hawk Cuckoo (*Hierococcyx sparverioides*), rejected 25% of blue model eggs and 46.1% of white model eggs; and the Chestnut Thrush (*Turdus rubrocanus*) and the Chinese Thrush (*T. mupinensis*), in which cuckoo parasitism has not been recorded, rejected 41.1 and 83.3% of blue model eggs, respectively. There were no significant differences in the egg rejection among them, although the Chinese Thrush showed the highest rate of egg rejection.

Conclusions: This study indicates that the egg recognition ability of cuckoo hosts has no correlation with the actual parasitism rate of cuckoos. We suggest that the egg recognition ability of the two potential host species may have been retained from a parasitic history with the cuckoo, while the two common host species have developed their egg rejection abilities due to current parasitism pressure. In addition, our study highlights the importance of the multi-cuckoo parasite system for better understanding the selection pressure of parasitism on the evolution of host egg recognition abilities.

Keywords: Anti-parasitic strategy, Cuckoo parasitism, Egg rejection, Large Hawk Cuckoo, Potential host

Background

Brood parasitism is a special breeding behavior of some cuckoo species where, instead of building their own nests, cuckoos lay their eggs in the nests of host birds, which hatch their eggs and raise their chicks (Payne 1977). Host birds pay a high reproductive cost for this. During parasitism, cuckoos take 1–2 eggs away from the host. After hatching, cuckoo chicks sometimes remove eggs or other chicks from the nest, and often get more food due to their superior physicality and begging sounds, thus defeating other host chicks in the nest (Davies 2000). Under this selection pressure hosts develop anti-parasitic strategies to prevent cuckoo parasitism at all breeding stages (Davies 2011; Soler 2014a). At the egg stage, many hosts recognize and reject parasitic eggs that are different from their own. This is one of the most effective and important anti-parasitic strategies (Davies 2000; Soler 2014a). As the host's egg recognition ability develops, parasites develop more precise "deceptive" behaviors, such as mimicking the host's eggs in color (Brooke and Davies 1988; Yang et al. 2010).

The host's egg recognition ability usually depends on the history of parasitism (Peer and Sealy 2004), parasitism selection pressure (Davies and Brooke 1988), and

*Correspondence: sunyh@ioz.ac.cn; liangwei@hainnu.edu.cn
[1] Ministry of Education Key Laboratory for Ecology of Tropical Islands, College of Life Sciences, Hainan Normal University, Haikou 571158, China
[2] Key Laboratory of Animal Ecology and Conservation Biology, Institute of Zoology, Chinese Academy of Sciences, Beijing 100101, China

tradeoffs in anti-parasitic behaviors (Davies and Brooke 1988; Davies et al. 1996). Apart from Common Cuckoo hosts (Moksnes et al. 1991), many potential hosts, including some cavity-nesting birds such as tits (Paridae), can also recognize and reject foreign parasitic eggs (Liang et al. 2016; Yang et al. 2019a). The hosts may have been parasitized in the past (e.g. Peer et al. 2007), or others within their lineage (Peer et al. 2011). This is because traits that do not decrease individual fitness may be maintained over long periods of time even in the absence of selection pressures (Peer and Sealy 2004). Numerous studies show that currently non-parasitized potential host species may have a rejection rate of nearly 100% (Soler 2014b). Therefore, it would be inaccurate to assume that egg rejection ability is driven by coexistence with brood parasites (Soler 2014a). For example, Yang et al. (2014) revealed that the Red-billed Leiothrix (*Leiothrix lutea*), a host of the Common Cuckoo (*Cuculus canorus*), was introduced 150 years ago to Hawaii where there was no cuckoo breeding, but it retained a strong egg rejection ability similar to that at its origin. Many other host species may retain rejection behavior in the absence of parasitism (Underwood et al. 2004; Lahti 2006; Medina and Langmore 2015).

Brood parasitism is generally regarded as the main driving force for the evolution of egg recognition ability. Higher parasitism selection pressure from cuckoos results in a stronger egg recognition ability of the host (Davies and Brooke 1988). Gärtner (1982) found that the Marsh Warbler (*Acrocephalus palustris*), a common host of the cuckoo, showed a high egg rejection rate (86.8%) to non-mimetic eggs. However, our understanding of the relationship between parasitism selection pressure and actual parasitism rate is limited. A recent study showed that perceived parasitism risk did not translate into realized differences in actual parasitism selection for Barn Swallows (*Hirundo rustica*) (Li et al. 2020). Therefore, the comparison of egg rejection in parasitized cuckoo hosts versus non-parasitized potential host species is of great significance for understanding the evolution of the egg recognition ability of hosts.

As a host's egg recognition ability develops, cuckoos lay eggs that are more similar to host eggs in color and shape (Brooke and Davies 1988; Davies 2000). However, recognition errors can occur when hosts attempt to reject mimetic eggs (Røskaft et al. 2002; Stokke et al. 2002); the host may accidently reject one or more of its own eggs (Davies and Brooke 1988). Davies et al. (1996) suggested that Reed Warblers (*Acrocephalus scirpaceus*) accept mimetic eggs when the parasitism rate is below 19–41% but reject when the parasitism rate is above this.

Scholars have recently examined whether thrushes are suitable hosts for cuckoos and the evolution of their egg recognition ability (Grim et al. 2011; Samăs et al. 2014; Soler 2014b; Ruiz-Raya et al. 2016). Insectivorous birds that have large populations and build open nests are generally considered suitable hosts for cuckoos (Soler et al. 1999). However, thrushes as suitable hosts are rarely parasitized by cuckoos in Europe (Moksnes and Røskaft 1995; Grim et al. 2011). Studies have shown that potential thrush hosts demonstrate high rejection rates of foreign eggs. The rejection rates of Song Thrushes (*Turdus philomelos*) and Blackbirds (*T. merula*) were found to be 58.3 and 66.7%, respectively (Grim and Honza 2001). Soler et al. (2015) found that the rejection rate of Blackbirds was 71.4%. Recent studies in China have even found that the rejection rate of Grey-backed Thrushes (*Turdus hortulorum*) to foreign eggs is almost 100% (Yang et al. 2019b; Zhang et al. 2019).

Unlike the single-cuckoo system in Europe, there are 17 species of parasitic cuckoos of different sizes in China (Yang et al. 2012; Zheng 2017). In our study area alone, there are five species of cuckoos, namely the Large Hawk Cuckoo, the Common Cuckoo, the Himalayan Cuckoo (*C. saturatus*), the Lesser Cuckoo (*C. poliocephalus*), and the Indian Cuckoo (*C. micropterus*) (Sun et al. 2008).

In this study, we investigated cuckoo parasitism in four bird species in a multiple-cuckoo system in China, namely the Chestnut Thrush (*Turdus rubrocanus*), the Chinese Thrush (*T. mupinensis*), the Elliot's Laughingthrush (*Trochalopteron elliotii*), and the White-bellied Redstart (*Luscinia phoenicuroides*). Our aims were to compare egg recognition abilities among the Elliot's Laughingthrush (a host of the Large Hawk Cuckoo), the White-bellied Redstart (a host of the Common Cuckoo), and two non-parasitized potential host species and, to examine whether their egg rejection rates are related to the actual cuckoo parasitism rate. We propose that if the egg rejection rate of the non-parasitized potential host species is lower than the parasitized host species, it indicates that parasitism has an important influence on the evolution of a host's egg recognition ability, and that egg rejection ability is related to parasitism rate. However, if their egg rejection rates are not significantly different, it suggests that egg recognition ability is not directly related to actual parasitism rate.

Methods

Study area and study species

We conducted this study from April to August in 2018 and 2019 in a farmland landscape at the northern edge of the Lianhuashan National Nature Reserve, Gansu, central China (34.67°N, 103.50°E). The area of the reserve is approximately 12,000 ha, with an average annual temperature of 5.1–6.0 °C and an average annual rainfall of approximately 650 mm. The altitude ranges between

2000 and 3500 m, with the main peak being 3578 m high (Sun et al. 2008).

The Chestnut Thrush (Turdidae: Passeriformes), has a medium-sized body (23–28 cm, 85–120 g; Zhao 2001), and is distributed throughout the Indian subcontinent, the Indochinese Peninsula, as well as the southwest and southeast coastal areas of China (Collar 2005). In the study area, the Chestnut Thrush is one of the most common bird species, mainly inhabiting montane broadleaf forests and mixed coniferous forests at an altitude of 2000–3500 m (Zhao and Sun 2016). Its breeding season is from April to August, and nesting starts from late April to early May. Its nest is 3 m high with poor concealment. The clutch size is 2–4 eggs with egg color being light blue with brown spots (Hu et al. 2017).

The Chinese Thrush (Turdidae: Passeriformes), has a medium-sized body (20–24 cm, 69–74 g; Zhao 2001), and is distributed throughout Eurasia, North Africa, the Indochinese Peninsula, as well as the southeast coastal areas, north, and northwest of China (Collar 2005). In the study area, the Chinese Thrush is relatively scarce and often remains hidden, making it difficult to observe. There is limited data on the reproduction of Chinese Thrushes (Liu et al. 2003). There have been no reports of cuckoo parasitism in the above two thrush species (Zhao and Sun 2016).

The Elliot's Laughingthrush (Leiothrichidae: Passeriformes) has a medium-sized body (22–25 cm, 49–72 g; Zhao 2001), and is endemic to China (Zheng 2017). Nests are usually built on smaller spruce trees at a height of 1.56 ± 0.38 m. Its average clutch size is 3.4 ± 0.5, with an incubation period of 14 days (Jiang et al. 2007; Liu and Sun 2016). In the study area, the Elliot's Laughingthrush is an important host of the Large Hawk Cuckoo (laying a mimetic blue egg), with a parasitism rate of 8.3% (Hu et al. 2013a).

The White-bellied Redstart (Turdidae: Passeriformes), is smaller than the above three species (16–19 cm, 19–27 g; Zhao 2001), and distributed in the central and western regions of China, the Himalayas, India, and Myanmar. The species mainly inhabits shrubs at an altitude of 1200–4500 m. Its breeding season is from May to August. The height of its nest is 0.4–1.5 m; and its clutch size is 2–4 (Lu et al. 2010). In the study area, the parasitism rate of Common Cuckoos (laying a mimetic blue egg) in White-bellied Redstarts can reach 16.4% (Hu et al. 2013b).

Egg rejection experiments

During the breeding season, we systematically searched for the nests of four bird species in the study area. After nests were identified, they were checked on a regular basis (every second day) and reproductive parameters were recorded, including nesting date, clutch size, incubation period, parasitic cuckoo species, and parasitism rate. Following the experimental methods of Moksnes et al. (1991) and Yang et al. (2019a), a blue model egg was added directly to the nests of the four species before mid-incubation (Fig. 1). However, the eggs of the Elliot's Laughingthrush were also blue. To avoid the influence of non-mimetic blue model eggs on the rejection rate of hosts due to similarity in color with host eggs, we included another treatment in which a white model egg was added directly to the nest of Elliot's Laughingthrushes to further test their egg recognition ability. The Chestnut Thrush showed a moderate rejection rate (54%) to foreign non-mimetic blue model eggs in a previous study (Yi et al. 2020). Previous work showed that the presence of parasites near hosts' nests (Moksnes and Røskaft 1989; Moksnes et al. 2000; Bartol et al. 2002; Davies et al. 2003) or nest sanitation (Yang et al. 2015c) may increase the rejection of parasitic eggs. To verify whether these two methods can affect the egg rejection rate of the Chestnut Thrush, in the present study, we developed two treatments to further test the egg recognition ability of the Chestnut Thrush. In the first treatment, a Large Hawk Cuckoo dummy (37 cm in body length) was placed 0.5 m near the nest for about 20 min, after which a blue model egg was added to the nest. In the second treatment, a blue model egg and half of a peanut shell were added to the nest at the same time (also see Yang et al. 2015c). Experimental nests were then examined on the 3rd and 6th day. If the model egg remained in the nest and the host did not abandon the nest by the 6th day, the model egg was considered to be accepted; however, if the model egg disappeared or was pecked, and parent birds did not abandon the nest, the model eggs were considered to be rejected. Nests that were preyed on or deserted within 6 days were not included in the experimental results. Except that one nest of the Elliot's Laughingthrush was included in both blue and white model egg treatments, whereas the other nests were only included in one treatment (Yang et al. 2019a).

Data analysis

Statistical analyses were performed using IBM SPSS 25.0 for Windows (IBM Inc., USA). The Chi square test and Fisher exact test were used to compare the rejection rate of model eggs among different groups. Bonferroni correction was used to adjust the test level to $\alpha = 0.005$ for comparison within the analysis groups. All tests were two-tailed, with statistical significance

Fig. 1 Photos of blue model egg in the nests of the four species (**a** Chestnut Thrush, **b** Chinese Thrush, **c** Elliot's Laughingthrush and **d** White-bellied Redstart)

at $p < 0.05$. The data are expressed as mean ± standard deviation (Mean ± SD).

Results

In 2018 and 2019, we found 95 and 81 Chestnut Thrush nests, 15 and 18 Chinese Thrush nests, and 8 and 7 White-bellied Redstart nests, respectively. No cuckoo parasitism was observed in these nests. There were 31 and 16 nests of the Elliot's Laughingthrush, respectively, among which 3 and 2 nests were parasitized, giving a two-year parasitism rate of 10.6%.

We found that the Chestnut Thrush did not reject more model eggs following exposure to a Large Hawk Cuckoo dummy ($n = 13$; Chi square tests, $\chi^2 = 2.228$, df = 1, $p = 0.136$) or when eggs were added together with a stimulus (half of a peanut shell) ($n = 21$; Chi square tests, $\chi^2 = 0.241$, df = 1, $p = 0.623$) compared with when eggs were added alone (54%, $n = 50$; Yi et al. 2020). As there was no significant difference between the two treatments (Fisher exact tests, $p = 0.477$) (Table 1), the results from both were integrated for comparison with the other three bird species.

Table 1 Rejection rates of four bird species in response to experimental parasitism

Species	Nest type	Experimental egg type	Rejected/experimental nest (rejection rate, %)	Rejection time (days)
Chestnut Thrush	Open	Blue model egg + Large Hawk Cuckoo dummy	4/13 (30.7)	2.2 ± 1.3 (range 1–4)
Chestnut Thrush	Open	Blue model egg + half peanut	10/21 (47.6)	3.0 ± 2.0 (range 1–6)
Chinese Thrush	Open	Blue model egg	15/18 (83.3)	2.0 ± 1.7 (range 1–6)
Elliot's Laughingthrush	Open	Blue model egg	2/8 (25)	3.5 ± 2.5 (range 1–6)
Elliot's Laughingthrush	Open	White model egg	6/13 (46.1)	1.0 ± 0.0 (range 1)
White-bellied Redstart	Open	Blue model egg	6/9 (66.6)	4.3 ± 1.7 (range 1–6)

We found that 41.1% ($n=34$) of Chestnut Thrushes recognized non-mimetic blue model eggs. Chestnut Thrushes removed the model eggs with their bills and did not abandon their nests during the experiment. Among the Chinese Thrushes, 83.3% ($n=18$) recognized model eggs (Table 1). The rejection rates of Elliot's Laughingthrushes to non-mimetic blue and white model eggs were 25% ($n=8$) and 46.1% ($n=13$), respectively (Table 1). The rejection rate of White-bellied Redstarts to blue model eggs was 66.6% ($n=9$; Table 1). In one Elliot's Laughingthrush nest, the blue model egg was pecked, leaving many marks, but not thrown away. However, in all the other nests, Elliot's Laughingthrushes rejected foreign eggs by removing them with their bills. The five bird-egg combinations had significantly different rejection rates (Fisher's exact test, $\chi^2=10.032$, $p=0.015$). Pairwise comparison within the group showed that there were no significant differences between any two groups (Fisher's exact test, $\chi^2=12.649$, $p=0.011$), while Elliot's Laughingthrushes exhibited a higher rejection rate with white model eggs compared to with blue ones, but rejection rates were not statistically different ($p=0.40$).

Elliot's Laughingthrushes always rejected white model eggs on the day they were added to the nest, while the other hosts rejected eggs within 1–6 days (Table 1).

Discussion

We studied four species of bird, the Chestnut Thrush, the Chinese Thrush, the Elliot's Laughingthrush, and the White-bellied Redstart, which all bred in the same region and built open nests. The Chestnut Thrush had the largest population and most nests. Moreover, the nests of the two thrush species were large and obvious. However, we found that the Elliot's Laughingthrush was the only species parasitized by the Large Hawk Cuckoo, while no cuckoo parasitism was observed for other three species during the 2 years' study period. There would be a possibility that some parasitic cuckoo eggs could be rejected before we found them or checked them, as we found that the Chestnut Thrush had a moderate ability to recognize non-mimetic eggs, while the Chinese Thrush of the same genus had a strong egg recognition ability. The Elliot's Laughingthrush and the White-bellied Redstart, which are hosts of the Large Hawk Cuckoo and the Common Cuckoo, respectively, also had a moderate ability to recognize non-mimetic eggs. However, further analysis revealed that there were no significant differences in the recognition ability of the four bird species.

Nest sanitation may be a pre-adaptation in the evolution of egg rejection behavior (Rothstein 1975; Moskát et al. 2003). To test this, Yang et al. (2015c) examined model egg rejection rates of Barn Swallows (*Hirundo rustica*), a host of the Common Cuckoo, when blue model eggs were added alone or with half of a peanut shell. They found that the egg rejection rate of the latter was higher than that of the former. Moreover, when hosts detect the presence of parasites near their nests, they increase the number of return visits to the nest to improve the recognition and rejection of parasitic eggs (Moksnes and Røskaft 1989; Moksnes et al. 2000; Bartol et al. 2002; Davies et al. 2003). To verify whether these two methods can affect the egg rejection rate of the Chestnut Thrush, we either added half of a peanut shell and a blue model egg to nests at the same time, or added a blue model egg following exposure of the nest to a cuckoo dummy. However, we found that there was no significant difference in egg rejection ability between the two treatments.

In our study area, the Elliot's Laughingthrush and the White-bellied Redstart are parasitized by the Large Hawk Cuckoo and the Common Cuckoo, respectively (Hu et al. 2013a, b). However, field observations have found no evidence of cuckoo parasitism in the Chestnut Thrush or the Chinese Thrush (Zhao and Sun 2016; Hu et al. 2017). Our results show that the Chestnut Thrush has a moderate egg rejection ability, which is similar to results from European studies of the Song Thrush and the Blackbird (Grim and Honza 2001). Conversely, we show that the Chinese Thrush has a strong egg recognition ability, which is similar to that of the Spanish Blackbird (Soler et al. 2015; Ruiz-Raya et al. 2016) and the Grey-backed Thrush in eastern China (Yang et al. 2019b; Zhang et al. 2019). Many potential hosts, even if not parasitized currently, may have retained an ability to reject eggs from a history with the parasite (Peer and Sealy 2004). Therefore, the two thrush species examined in our study may have at one stage been parasitized by cuckoos, and therefore developed and retained their egg rejection ability.

There are many species of cuckoos in China, as well as numerous host birds to choose from (Yang et al. 2012). In our study area, the Elliot's Laughingthrush is a common host of the Large Hawk Cuckoo, with a parasitism rate of up to 8.3% (Hu et al. 2013a). Our results further confirmed similar parasitism rate. Elliot's Laughingthrush eggs are blue with brown spots. Large Hawk Cuckoo eggs are a similar blue but are spotless. This indicates that the Large Hawk Cuckoo may have mimicked its host, the Elliot's Laughingthrush, in egg color. This may make it difficult for the Elliot's Laughingthrush to recognize parasitic eggs, thereby enabling the Large Hawk Cuckoo to parasitize it successfully. We found that for the Elliot's Laughingthrush, the rejection rate of blue model eggs was lower than that of white model eggs, likely due to their similar color to host eggs. Moreover, Large Hawk Cuckoos in southern China lay pure white eggs, which likely mimic the egg color of another host—the White-browed Laughing Thrush (*Garrulax sannio*) (see Fig. 1 in

Yang et al. 2015a). This shows that parasitism selection pressures can drive differences in anti-parasitism strategies (Yang et al. 2015b). In our study area, the White-bellied Redstart is a host of the Common Cuckoo, with an actual parasitism rate of 16.4% (Hu et al. 2013b). However, some White-bellied Redstarts were also parasitized by the Large Hawk Cuckoo (Huo et al. 2016). This indicates that one host may be parasitized by many species of cuckoos at the same time, which suggests that in a multiple-cuckoo system, a bird species considered an unsuitable host for one cuckoo species (e.g., Common Cuckoo) may be a suitable host (or common host) for another cuckoo species. In our two-year study, we found no evidence of White-bellied Redstarts being parasitized by cuckoos, for which there may be two reasons. First, the host bird might have recognized and rejected the parasitic eggs of cuckoos, and therefore parasitic nests were not observed. Some hosts reject parasitic eggs immediately after parasitism, which can lead to low parasitism rates (Rothstein 1977; Sealy et al. 1995). Second, cuckoo parasitism may be rare or highly variable, and therefore was missed in our study.

Recognizing and rejecting foreign eggs is one of the most direct and effective ways for hosts to combat brood parasitism (Davies 2000). By testing the egg recognition ability of two cuckoo host species, we found that both the Elliot's Laughingthrush and the White-bellied Redstart had a moderate ability to recognize non-mimetic eggs, which may be due to the selection pressure of parasitism. However, we found no significant difference in their egg recognition abilities. We suggest that the egg recognition ability of potential host species may be retained from a parasitic history with cuckoos, whereas currently used hosts have developed an egg rejection ability due to parasitism pressure, therefore egg recognition ability of hosts has no significant correlation with actual cuckoo parasitism rate.

Conclusions

We found that the Chestnut Thrush, the White-bellied Redstart, and the Elliot's Laughingthrush had moderate egg recognition abilities, while the Chinese Thrush showed a strong egg recognition ability. Both parasitized cuckoo hosts and non-parasitized potential host species could recognize and reject foreign non-mimetic eggs at a similar rate. We suggest that the egg recognition ability of the two potential host species of thrushes may be retained from a parasitic history with cuckoos, while the common hosts have developed egg rejection abilities because of actual parasitism pressure. There was no direct correlation between the host's egg recognition ability and the actual parasitism rate of cuckoos. In Europe, only one species of cuckoo, the Common Cuckoo, may parasitize thrushes. In contrast, in the multiple-cuckoo system of China, it is unclear whether the two thrush species may be parasitized by other cuckoo species, such as the Large Hawk Cuckoo and the Indian Cuckoo. Moreover, the ability of hosts to recognize cuckoo chicks during feeding remains to be determined in our study region. This is required in order to better understand the selection pressure of parasitism on the evolution of egg recognition abilities in hosts. The present study highlights the importance of the multiple-cuckoo system for better understanding the selection pressure of parasitism on the evolution of host egg recognition abilities.

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Authors' contributions
WL and YHS designed the study; TY carried out field experiments and performed data analyses; TY and WL wrote the draft manuscript, and YHS helped improve the manuscript. All authors approved the final submission. All authors read and approved the final manuscript.

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Availability of data and materials
The datasets used in the present study are available from the corresponding author on request.

Ethics approval and consent to participate
The experiments reported here comply with the current laws of China. Fieldwork was carried out under the permission from Lianhuashan National Nature Reserve, Gansu, China. 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-2014-005).

Consent for publication
Not applicable.

Competing interests
The authors declare that they have no competing interests. The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

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