



Egg rejection and egg recognition mechanism of chestnut thrushes (*Turdus rubrocanus*)



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ABSTRACT

Recognizing and rejecting foreign eggs is one of the most effective anti-parasite strategies for hosts in avian brood parasitism. Studies have shown that most cuckoo (*Cuculus* spp.) hosts have evolved egg recognition abilities. Although some open-nesting birds, especially thrushes belonging to the family Turdidae, are rarely parasitized by cuckoos, they still have high egg recognition ability. This evolutionary selection pressure on egg recognition is currently controversial. Previous studies on egg recognition of thrushes have mainly been carried out in Europe in a single-cuckoo system. In this study, chestnut thrushes (*Turdus rubrocanus*), which are distributed in a multiple-cuckoo system in China, were used to test their egg rejection and egg recognition mechanism. Our results showed that chestnut thrushes had a rejection rate of 54 % for non-mimetic blue model eggs, showing moderate egg recognition ability. Their egg recognition was true recognition, which relied on a memory template; chestnut thrushes could accurately reject foreign eggs in their nests. This study added the second case to report the egg recognition mechanism of thrushes in the Turdidae family and showed that the evolution of egg recognition ability of chestnut thrushes was likely a retained anti-parasitic strategy because of being parasitized by cuckoos in the past.

1. Introduction

Avian brood parasitism refers to a special breeding strategy of some birds. Specifically, in this behaviour, certain birds do not build their own nests, but instead lay their eggs in the nests of other birds and let the hosts hatch and feed their offspring (Payne, 1977). Avian brood parasitism can be classified into conspecific brood parasitism (CBP) and interspecific brood parasitism (IBP) (Davies, 2000). Brood parasitism, especially IBP, brings a huge breeding cost to the hosts and forces the hosts to evolve a series of anti-parasitic strategies to deal with the parasitism (Davies, 2000; Soler, 2017; but see Samaš et al., 2018, 2019). Egg recognition and rejection is one of the most important behaviours for hosts against brood parasitism (Davies, 2000; Soler, 2014a). Although nest usurpation (Weeks, 1980; Peer and Bollinger, 1998) and colonial breeding (Fredrickson and Weller, 1972; Schaffner, 1990) may also lead to the evolution of egg recognition in birds, brood parasitism is the most important selection pressure for egg recognition and egg rejection behaviours during evolution (Soler, 2014b). For example, some birds have a low ability to recognize foreign eggs because they have different foraging habits from cuckoos (*Cuculus* spp.), or their nests are difficult to be accessed by cuckoos (Davies et al., 1989;

Moksnes et al., 1991; Liu et al., 2019). In another study, a population of vinous-throated parrotbill (*Sinosuthora webbiana*) in Taiwan showed significantly less egg rejection than the population in mainland China, where there is high parasitism from common cuckoos (*Cuculus canorus*) (Yang et al., 2015).

Insect-eating birds with a large population that live in open nests have been generally considered as suitable hosts for cuckoo species (Soler et al., 1999; Davies, 2000; but see Yang et al., 2013). However, blackbirds (*Turdus merula*) and song thrushes (*T. philomelos*), which are found in Europe in large populations, have high breeding densities, and build open and clearly visible nests, are rarely parasitized by cuckoos (Moksnes and Røskaft, 1995; Soler et al., 1999; Grim et al., 2011). Blackbirds and song thrushes have relatively high foreign egg rejection rates (Grim and Honza, 2001). Soler et al. (2015) also indicated that the rejection rate of non-mimetic eggs was as high as 71.4 %. Therefore, the high egg rejection in thrushes, which are currently rarely parasitized by cuckoos, has attracted the interest of researchers in the field. Since thrushes rarely occupy conspecific nests and are not colonial breeders, the evolution of egg recognition is mainly considered from the perspective of brood parasitism. However, it is controversial whether CBP or IPB is the major selection pressure on the evolution of egg rejection

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behaviour (Samaš et al., 2014; Soler, 2014b).

Samaš et al. (2014) showed that rejection of conspecific foreign eggs by blackbirds and song thrushes reached 20–40 %. Therefore, they suggested that blackbirds and song thrushes evolved egg recognition ability to cope with CBP rather than IBP. Grim and Honza (2001) also showed that CBP played an important role in the evolution of egg rejection behaviour of blackbirds and song thrushes.

In contrast, Rothstein and Robinson (1998) argued against CBP as an important selection pressure for the evolution of egg rejection. Also, Soler (2014b) did not support the idea that egg recognition ability evolved from CBP and refuted the opinions of Samaš et al. (2014) based on the analysis of evolutionary pressure and parasitic history. Firstly, the appearance of conspecific eggs was similar; therefore, egg recognition ability evolving from CBP would be rather difficult (Reeve, 1989). In addition, IBP hosts have greater fitness costs than CBP hosts (Petrie and Møller, 1991; Davies, 2000; Lyon and Eadie, 2008). Therefore, the CBP and IBP hosts would not have the same anti-parasitic strategies. Secondly, previous studies have shown that some features can be retained in the absence of selective pressure. For example, many potential hosts still had high egg rejection rates even though they were not parasitized (Peer and Sealy, 2004). Thirdly, studies showed that thrushes were aggressive towards cuckoos, suggesting that both thrushes and cuckoos had a history of co-evolution (Grim et al., 2011). Lastly, the probability of thrushes being parasitized by conspecific species was relatively low, which was insufficient to support the hypothesis that CBP promoted the evolution of egg recognition (Soler, 2014b). Ruiz-Raya et al. (2016) demonstrated that thrushes had high rejection rates (80–100 %) of foreign eggs from different species, even under the risk of CBP. Furthermore, the rejection rate of foreign eggs from conspecific species was less than 13 %, which supported the hypothesis of IBP (Ruiz-Raya et al., 2016).

In addition, previous work has shown the presence of IBP in thrushes. Moksnes and Røskoft (1995) analysed cuckoos eggs collected in European museums and found that 21 blackbird eggs, 11 song thrush eggs, four ring ouzel (*Turdus torquatus*) eggs, three fieldfare (*T. pilaris*) eggs and two redwing (*T. iliacus*) eggs were among the cuckoos eggs. Glue and Morgan (1972) also reported that thrushes raised a young cuckoo until it left the nest. Zhou et al. (2001) reported the first case in China in which thrushes were parasitized by Indian cuckoos (*Cuculus micropterus*). A study across Europe showed that common cuckoos selected hosts for brood parasitism with either bigger or smaller body sizes rather than species with intermediate sizes (Stokke et al., 2018).

Unlike a single-cuckoo system in Europe, parasitic cuckoos in China are very diverse (up to 17 species; Yang et al., 2012; Zheng, 2017), making it possible for thrushes to be parasitized. Recent studies in China indicated that grey-backed thrushes (*Turdus hortulorum*) show egg polymorphism and exhibit 100 % rejection towards non-mimetic eggs, but low rejection towards conspecific eggs (Yang et al., 2019; Zhang et al., 2019). Egg polymorphism in hosts is regarded as a specific adaptation against cuckoo parasitism; it has evolved and been maintained under selection from cuckoo parasitism but decreases in the absence of such selection pressures (Yang et al., 2017). This further suggested that thrushes were likely parasitized by cuckoos, thereby preserving their egg rejection ability (Yang et al., 2019). The common cuckoo is the only cuckoo species found in most parts of Europe, and the population size of thrushes in Europe is relatively large; therefore, thrushes may not be the main host of common cuckoos (Stokke et al., 2018). However, in China, thrushes are likely to be parasitized by larger cuckoos, such as large hawk cuckoos (*Hierococcyx sparveroides*) and Indian cuckoos. Clearly, the evolution of egg recognition in thrushes requires further validation by additional studies of various species and populations.

Although many studies have reported egg recognition of thrushes (Moskát et al., 2003; Samaš et al., 2014; Soler et al., 2015; Ruiz-Raya et al., 2016, 2019), the egg recognition mechanism of thrushes has only been reported for American robins (*Turdus migratorius*) (Rothstein,

1975). There are two known mechanisms of egg recognition in birds (Rothstein, 1974, 1975; Hauber and Sherman, 2001): (1) true recognition; birds can truly recognize their own eggs by using their own eggs as memory templates in order to distinguish the foreign eggs (Hauber et al., 2006; Yang et al., 2014a; Wang et al., 2015), and (2) recognition by discordancy; birds reject the eggs in the nest according to inconsistency. The advantages of the first egg recognition mechanism are that the true recognition of foreign eggs is not limited by the number of eggs and there are no recognition errors, especially when facing multiple parasitic cuckoos. In the second mechanism, the eggs with a significant inconsistency in their appearance, or the type of egg that is fewer in number within the nest, are rejected (Bán et al., 2013; Stevens et al., 2013; Yang et al., 2014a).

In this study, we aimed to investigate the CBP and IBP rates of chestnut thrushes (*Turdus rubrocanus*) and to identify their egg recognition ability and mechanism. We hypothesized that chestnut thrushes can accurately recognize and reject foreign eggs, if the egg recognition mechanism is true recognition (template recognition), regardless of whether they have no own eggs in the nest, or whether the majority of the eggs in the nest are their own.

2. Materials and methods

2.1. Study area and study species

We conducted this study from April to August in the years 2018 and 2019 in farmlands on the northern edge of Lianhuashan National Nature Reserve, Gansu, Central China (34.67 °N, 103.50 °E). The nature reserve, with an approximate area of 12,000 ha, has an average annual temperature of 5.1.6.0 °C, an average annual precipitation of approximately 650 mm and an altitude range of approximately 2000–3500 m with a main peak elevation of 3578 m (Sun et al., 2008). There are five cuckoo species distributed alongside chestnut thrushes within the study area, including large hawk cuckoos, common cuckoos, Indian cuckoos, Himalayan cuckoos (*Cuculus saturates*) and lesser cuckoos (*C. poliocephalus*) (Sun et al., 2008).

The chestnut thrush has a moderate body size (85–100 g), and is distributed in the Indian subcontinent, the Indochina peninsula and south China (Collar et al., 2005). This bird was one of the most abundant species in our study area. It mainly inhabits broadleaf and mixed forests with conifers and broadleaf trees at an altitude of 2000–3500 m (Zhao and Sun, 2016). The breeding season of chestnut thrushes is from April to August, and their nests are usually 1–3 m above the ground with poor concealment, and each nest contains 2–4 eggs, which are light blue in colour with brown spots (Fig. 1a, b; Hu et al., 2017).

2.2. Field experiment

Nests of chestnut thrushes were systematically searched in the study area and nest inspection was undertaken to record the breeding parameters of chestnut thrushes, such as the nesting date, egg-laying time, incubation time, and cuckoo parasitism rate. When a well-constructed nest was found, it was monitored once every day or within two days. Following Yang et al. (2019), we directly placed a blue model egg (Fig. 1c) or a conspecific egg (from another nest with similar colour) in nests of chestnut thrushes during the incubation period (before mid-incubation) to simulate cuckoo or CBP parasitism, respectively. Videos of response of chestnut thrushes to alien eggs were also recorded using mini-cameras (Uniscom-T71, 70 mm × 26 mm × 12 mm; Mymahdi Technology Co. Ltd., Shenzhen, China) for 1–2 h for each nest. Subsequently, the experimental nests were checked once every day over six consecutive days. If the model eggs or conspecific eggs were still in the nests, they were considered accepted by the host. If model eggs or conspecific eggs disappeared, or if they were pecked by the host, they were considered to be rejected. The nests where the eggs were preyed upon, or the nests that were destroyed before day 6 were excluded from



Fig. 1. Nest (a) and egg (b) of the chestnut thrush, with examples of an experimental non-mimetic blue model egg (c), experimental groups for the T1 group, (d), which refers to the experimental group with “2 + 2” or “3 + 3”, implying that experimental eggs were the same as host eggs, and T2 group (e), which refers to the experimental group with “0 + 3” or “0 + 4”, implying that there are no host eggs in the experimental nests.

the analysis. Only one experiment was performed for each nest (see details in Yang et al., 2019).

After confirming that the focal chestnut thrushes recognized and discarded the blue model eggs, the egg recognition mechanism was further tested. In order to prevent chestnut thrushes from preserving the memory of the same blue model eggs, we used another type of eggs (i.e. commercially available eggs of the budgerigar, *Melopsittacus undulatus*) different from the blue model eggs, to test the egg recognition mechanism of chestnut thrushes. Following the methods described by Yang et al. (2014a), the first group of experiments (T1) was either “2 + 2” or “3 + 3”, i.e. keeping equal numbers of chestnut thrush and budgerigar eggs in the experimental nest (Fig. 1d). The ratio of budgerigar to the number of chestnut thrush eggs was adjusted to 1:1 by adding budgerigar eggs to the experimental nest. The second group of experiments (T2) was either “0 + 3” or “0 + 4”, which was conducted by replacing all chestnut thrush eggs with the same number of budgerigar eggs in the nest (Fig. 1e). All experimental nests were followed by monitoring nests for six consecutive days to record the response.

3. Results

3.1. Clutch size, IBP and CBP rate

A total of 95 and 81 nests of chestnut thrushes were found in the field in the years 2018 and 2019, respectively. There was no evidence of CBP or cuckoo parasitism as we did not observe either two eggs being laid on the same day or any cuckoo egg during the egg-laying period. The clutch size of chestnut thrushes was 3.12 ± 0.64 (mean \pm S.D., range: 2–4 eggs, $n = 34$ nests) in 2018 and 3.39 ± 0.49 (range: 3–4 eggs, $n = 33$ nests) in 2019. There was no significant difference in clutch size between the two study years (Mann-Whitney U Test, $Z = -1.772$, $P = 0.076$). The eggs of chestnut thrushes were 7.34 ± 0.83 g in egg mass (range: 4.89–7.84 g, $n = 34$ nests) and 30.74 ± 1.48 mm (length range: 25.95–33.43 mm) \times 21.77 ± 0.67 mm (width range: 20.48–23.08 mm) in egg size for the year 2018. The eggs were 7.2 ± 0.81 g in egg mass (range: 5.64–8.83 g, $n = 33$ nests), and 30.76 ± 1.33 mm (range: 27.97–33.83 mm) \times 21.64 ± 0.80 mm (range: 19.72–23.14 mm) in egg size for the year 2019. There was no significant difference in egg mass (Levene’s test, $F = 0.238$ $df = 65$, $P = 0.472$) or egg size (egg length: $F = 0.019$, $df = 65$, $P = 0.953$; egg

width: $F = 0.737$, $df = 65$, $P = 0.468$) between the two study years.

3.2. Egg rejection

The results of the egg rejection experiments showed that 54 % of chestnut thrushes had the ability to reject the non-mimetic blue model eggs ($n = 50$), showing a moderate level of egg rejection (Table 1). Chestnut thrushes directly removed the model eggs with their beaks and did not abandon any nest during the experiment. Among 27 rejected nests, most egg rejections occurred within one day (77.78 %, $n = 21$), one nest on the fourth day (3.7 %) and three nests on the sixth day (18.52 %). A total of 10 nests were tested using conspecific eggs and all nests accepted the foreign conspecific eggs. Therefore, the rejection rate of CBP eggs of the same colours was nil ($n = 10$, Table 1).

3.3. Egg recognition mechanism

In the T1 experimental group, chestnut thrushes completely recognized, rejected and discarded 100 % of the foreign eggs ($n = 14$, Table 1). In the T2 group, chestnut thrushes were able to accurately recognize and discard all the foreign eggs ($n = 17$, Table 1). Video recording showed that chestnut thrushes used their beaks to remove the foreign budgerigar eggs one by one, and all the rejection of real eggs was completed on the same day as the experiment. In the T1 group, chestnut thrushes returned to their nests after two foreign eggs were removed and continued incubation (ESM Video S1). No nest was deserted ($n = 14$) and no recognition errors or discarding of their own

Table 1

The probability of egg rejection by chestnut thrushes.

Experimental group	Egg rejection (%)	Number of nests tested
One conspecific egg	10 (0)	10
One blue model egg	27 (54)	50
T1	14 (100)	14
T2	17 (100)	17

Note: T1 refers to the experimental group with “2 + 2” or “3 + 3”, implying experimental eggs are the same as host eggs; T2 refers to the experimental group with “0 + 3” or “0 + 4”, implying there are no host eggs in the experimental nests.

eggs (rejection cost) were observed during the experimental period. Interestingly, in the T2 group, chestnut thrushes returned to their nests after all four foreign eggs were removed and continued incubation with an empty nest for up to 20 min, until their eggs were returned (within 20–30 min) (ESM Video S2). Two nests were deserted ($n = 17$) after the experiment and no recognition errors or rejection costs were observed. Interestingly, there were two exceptions: the hosts stayed in the empty nests for more than 10 min before abandoning the nests.

Of the 14 experimental nests in the T1 group, one nest was predated, one was deserted after the experiment, one partly hatched (one out of three eggs; 33.3 %), and 11 nests were successfully hatched. Of the 17 experimental nests in the T2 group, two nests were predated, two were deserted after the experiment, two partly hatched (three out of four eggs in one nest; 75 % and two out of three eggs in another nest; 66.6 %) and 11 nests were successfully hatched.

4. Discussion

In this study, breeding chestnut thrushes were common in the study area, and the nests of chestnut thrushes were relatively abundant, large and conspicuous. Our results indicated that chestnut thrushes had a moderate ability to reject non-mimetic eggs but showed no rejection towards conspecific eggs. In addition, chestnut thrushes showed true recognition (template recognition) and knew their own eggs. Similar to American robins (Rothstein, 1975), such a recognition mechanism meant that chestnut thrushes relied on the memory template to accurately recognize foreign eggs of parasitic birds and was independent of the ratio of their eggs to foreign eggs in their nests. Thus, our study added the second case to report the egg recognition mechanism of thrushes in the Turdidae family.

Unlike the single-cuckoo system in Europe, there were five cuckoo species distributed alongside chestnut thrushes within our study area, therefore, the possibility of cuckoo parasitism on chestnut thrushes was relatively high. For example, white-bellied redstart (*Luscinia phaenicuroides*) and Elliot's laughing thrush (*Trochalopteron elliotii*), distributed in the same study area, were parasitized by common cuckoos and large hawk cuckoos, respectively (Hu et al., 2013a, b). However, based on long-term field observations, chestnut thrushes were not found to be parasitized by cuckoos (Zhao and Sun, 2016; Hu et al., 2017). In this study, our results showed that chestnut thrushes had a moderate ability to reject foreign eggs, which was similar to the reported egg recognition ability of blackbirds and song thrushes in Europe (Grim and Honza, 2001), but lower than the egg rejection rates of blackbird populations in Spain (Soler et al., 2015; Ruiz-Raya et al., 2016) and grey-backed thrush populations in eastern China (Yang et al., 2019; Zhang et al., 2019).

CBP has been suggested to constitute an important selection pressure for the evolution of egg rejection (Rothstein and Robinson, 1998). Peer and Sealy (2000) found that great-tailed grackles (*Quiscalus mexicanus*) rejected 100 % of bronzed and brown-headed cowbird eggs and also rejected a low fraction of conspecific eggs, because this host had evolved sophisticated egg recognition abilities to recognize conspecific eggs that differed sufficiently from its own. Therefore, the evolutionary selection pressure on egg recognition by thrushes is still controversial. A study by Samaš et al. (2014) suggested that CBP promoted the evolution of egg recognition ability of thrushes. However, Soler (2014b) disagreed with the above point of view and found no evidence to support the evolution of thrushes in recognizing foreign eggs from CBP. Soler et al. (2015) further demonstrated that egg colour had no significant impact on the nest desertion rate of thrushes. In addition, Ruiz-Raya et al. (2016) showed that the rejection of parasitic foreign eggs from different thrush species is significantly higher than that of conspecific eggs, which supports the IBP hypothesis (see also Yang et al., 2019; Zhang et al., 2019). Our study showed that none of the chestnut thrush nests were parasitized by conspecific species, and there was no evidence of CBP in previous work in the same study area (Zhao et al., 2016; Zhao

and Sun, 2016, 2018; Hu et al., 2017). Thus, it is necessary to conduct an in-depth study to investigate their degree of hostility towards cuckoos and to determine whether chestnut thrushes could feed the young cuckoos in their nests (Grim et al., 2011). Such research would better explain why chestnut thrushes are rarely parasitized by cuckoos. We suggest that the egg recognition ability of chestnut thrushes is likely owing to the anti-parasitic strategy carried over from its history of being parasitized by cuckoos. For example, many potential hosts maintain egg rejection ability, which is an important anti-parasitic strategy, even without being parasitized currently due to their history of parasitism (Peer and Sealy, 2004). Additionally, a common cuckoo host, the red-billed leiothrix (*Leiothrix lutea*), was not parasitized by cuckoos in Hawaii since its introduction to Hawaii 100 years ago, but still had a strong egg rejection ability similar to its ability in its native range (Yang et al., 2014b).

Regardless of having their egg(s) as recognition template(s) in the nest, chestnut thrushes could accurately recognize and reject the foreign eggs and did not reject their own eggs. These results support the true recognition (template recognition) mechanism. Previous studies have shown that most hosts with egg recognition ability also use the template recognition mechanism (Soler, 2017). For example, Peer and Sealy (2001) showed that great-tailed grackles rejected all foreign model eggs and kept their own eggs. However, ashy-throated parrotbills (*Sinosuthora alphonsiana*) can reject parasitic eggs using both true recognition and recognition by discordancy mechanisms (Yang et al., 2014a). True recognition may be obtained genetically (Amundsen et al., 2002; Stokke et al., 2004) or through observational learning (Lotem et al., 1995; Moskát et al., 2010). However, further studies are necessary to confirm whether the true recognition mechanism of chestnut thrushes is innate or acquired by observing their own eggs the first time they breed.

In conclusion, this study showed that chestnut thrushes had moderate egg recognition and could recognize and reject foreign eggs that were similar in size and shape, but different in colour to their own eggs. However, the reason for being rarely parasitized by cuckoos in thrushes remains unknown. In addition, chestnut thrushes showed little recognition towards conspecific eggs. The egg recognition mechanism of chestnut thrushes was true recognition (template recognition) and they could accurately recognize parasitic foreign eggs even without having their own eggs as a control. We suggest that chestnut thrushes may have evolved the ability to recognize foreign eggs due to a history of parasitism by cuckoos and a legacy of employing an anti-parasitic strategy to cope with IBP rather than CBP.

Ethics

The experiments reported here comply with the current laws of China. Fieldwork was carried out with permission from the Lianhuashan National Nature Reserve Management Bureau, 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).

Data accessibility

The data used in this study are available in the Electronic Supplementary Materials.

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CRedit authorship contribution statement

Tingting Yi: Investigation, Data curation, Formal analysis, Writing - original draft. **Yue-Hua Sun:** Conceptualization, Resources, Writing - review & editing, Supervision. **Wei Liang:** Conceptualization, Validation, Methodology, Writing - review & editing, Supervision, Visualization.

Declaration of Competing Interest

The authors declare that they have no competing interests.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.beproc.2020.104158>.

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