Nest sanitation facilitates egg recognition in the common tailorbird, a plaintive cuckoo host

DEAR EDITOR,

Nest sanitation is a ubiquitous behavior in birds and functions to remove foreign objects that accidentally have fallen into their nests. In avian brood parasitism, the host's ability to recognize and reject parasitic eggs is a specific anti-parasitic behavior. Previous studies have shown that egg recognition may have evolved from nest sanitation behavior; however, few studies have offered evidence in support of this hypothesis. In the current study, we added one real white egg and one model egg to the nests of common tailorbirds (*Orthotomus sutorius*), the main host of plaintive cuckoos (*Cacomantis merulinus*), to explore the relationship between egg recognition ability in hosts and nest sanitation behavior. Results showed that common tailorbirds rejected both non-mimetic blue model eggs and mimetic white model eggs at a similar rate of 100%, but only rejected 16.1% of mimetic real white eggs. The egg rejection behavior of common tailorbirds towards both real and model eggs was consistent. However, when both blue model eggs and real white eggs were simultaneously added to their nests, the probability of rejecting the mimetic real white egg increased to 50%. The addition of blue model eggs not only increased the occurrence of nest sanitation behavior but also increased the ability to recognize and reject parasitic eggs. This suggests that nest sanitation may facilitate egg rejection in common tailorbird hosts.

Nest sanitation is an important and ubiquitous behavior in birds that results in the removal of foreign objects and waste materials from their nests. Birds swallow, transport, or bury nest objects to ensure cleanliness and thus reduce the risk of shell damage and chick infection by pathogens and parasitic worms (Guigueno & Sealy, 2012, 2017; Ibáñez‑Álamo et al., 2017). Birds not only remove chick feces, eggshells, unhatched eggs, and dead chicks but also foreign objects (Guigueno & Sealy, 2009; Moskát et al., 2003). In avian brood

parasitism, many hosts rely on differences in egg color, size, markings, and shape to differentiate between their own eggs and those that are parasitic (Davies & Brooke, 1988; Polačiková & Grim, 2010; Rothstein, 1975b, 1982), and thus identify such eggs as foreign objects to be discarded from the nest. For example, the American robin (*Turdus migratorius*) rejects and removes model eggs that deviate from their own in dominant color, size, and markings (Luro et al., 2018). This form of egg rejection could be considered as a type of nest sanitation behavior. Therefore, we propose the following question: Does egg rejection behavior in birds evolve from nest sanitation behavior? Nest sanitation may be an important stage in the evolution of egg recognition in hosts because nest sanitation, egg recognition, and parasitic egg rejection reduce the reproductive costs incurred from raising another bird's progeny (Davies & Brooke, 1989; Payne, 1977). Egg rejection in birds is usually achieved by grasping or puncturing the eggs with their beaks and removing the eggs from the nest (Moksnes et al., 1991; Rohwer & Spaw, 1988). Both egg rejection and nest sanitation behavior involve the removal of foreign or unwanted matter from the nest.

Rothstein (1975a) first proposed that nest sanitation behavior may be a pre-adaptation of egg rejection. Moskát et al. (2003) further proposed a hierarchal concept to explain the relationship between nest sanitation and egg rejection behavior: i.e., (1) host rejection of all non-egg-like objects is a general cleaning mechanism; and, (2) hosts that recognize their own eggs can differentiate between objects similar to their eggs and parasitic eggs. In other words, the greater the differences, e. g., in appearance, between the foreign object and the egg, the stronger the bird's ability to differentiate between them, and the more likely that the foreign objects will be rejected. An initial study of red-winged blackbirds (*Agelaius phoeniceus*) showed removal of model eggs that mimicked broken eggs but not rejection of parasitic cowbird eggs (Kemal & Rothstein, 1988; McMaster & Sealy, 1997). Yang et al. (2015a) added a peanut shell alongside a model egg in the

nests of barn swallows (*Hirundo rustica*), a host of common cuckoos (*Cuculus canorus*), and found that the probability of rejecting model eggs increased significantly in the presence of a half peanut shell. Furthermore, Yang et al. (2015b) showed that the rate of rejection of foreign eggs increased with the rate of rejection of non-egg-shaped objects in barn swallows. These results suggest a possible association between nest sanitation behavior and egg recognition in cuckoo hosts.

The study of Mermoz et al. (2016) on brown-and-yellow marshbirds (*Pseudoleistes virescens*) did not directly discuss the role of nest sanitation behavior in egg rejection by hosts but suggested that adding one spotted-blue artificial egg increased the rejection rate of cowbird eggs. However, when Peer (2017) followed the method of Yang et al. (2015a) and added a piece of flagging tape or a pinecone bract scale to the nest of red-winged blackbirds, they found that the addition of foreign material did not affect the host's rejection rate of cowbird eggs. Su et al. (2018) added peanut shells and model eggs to the open nests of brown-breasted bulbuls (*Pycnonotus xanthorrhous*) and found that nest sanitation behavior did not affect egg recognition ability in this species. Evidently, the effects of nest sanitation behavior on egg recognition differ among species, and thus the connection between these behaviors in birds remains unclear (Luro & Hauber, 2017). As such, further studies on more species are required to validate the role of nest sanitation behavior on the evolution of egg recognition and egg rejection behavior.

Most previous studies on the relationship between egg rejection ability and nest sanitation behavior have used non-egg-shaped objects to stimulate birds (Luro & Hauber, 2017; Peer, 2017; Su et al., 2018; Yang et al., 2015a). According to Moskát et al. (2003), the more dissimilar the shape of a foreign object compared to the host egg, the more likely that nest sanitation behavior will be elicited. However, although egg-shaped objects better simulate cuckoo eggs, few studies have used egg-shaped objects to stimulate nest sanitation behavior in hosts (Mermoz et al., 2016).

Common tailorbirds are one of the main hosts of plaintive cuckoos (*Cacomantis merulinus*) (Nahid et al., 2016; Payne, 2005; Tunheim et al., 2019; Yang et al., 2012). They are extremely sensitive to the appearance of foreign eggs and frequently reject eggs that exhibit a different color or pattern to their own (Yang et al., 2016). In the current study, using egg-shaped objects (i.e., mimetic real white eggs and non-mimetic blue and white model eggs), we tested whether egg recognition ability in common tailorbirds could be stimulated to examine the relationship between nest sanitation and egg rejection behavior. As egg-shaped objects can better simulate cuckoo eggs (Mermoz et al., 2016), we predicted that the addition of a real white egg together with a blue model egg would significantly increase the rejection rate of real white eggs compared to the group in which only real white eggs were added.

The study site is located at the Nonggang National Nature Reserve in Guangxi, southwest China (N22°13', E106°42') at an altitude of 150−650 m a. s. l.. The site has a typical subtropical monsoon climate with an annual mean

temperature of 20.8−22.4 °C and annual mean rainfall of 1 150−1 550 mm (Zhou & Jiang, 2008).

The study was conducted during the breeding season (March−September) in 2018. Common tailorbirds are one of the most abundant bird species in the study area and the main host for plaintive cuckoos, with a general parasitism rate of 17.0% (Yang et al., 2016). Common tailorbirds usually lay 4−5 brown-spotted blue or white eggs, with the plaintive cuckoos also laying eggs of similar (but not identical) color and pattern (Tunheim et al., 2019; Yang et al., 2016). Tailorbird hosts with blue clutches eject 100% of conspecific white eggs but accept 100% of conspecific blue eggs; similarly, tailorbird hosts with white clutches eject 100% of conspecific blue eggs and accept nearly all conspecific white eggs (Yang et al., 2016). The common tailorbird is a local resident species with a relatively long breeding season from mid-March until the end of September (Yang et al., 2016). These birds build nests in broad-leaf forests or shrubs at the edges of mountains by stitching together 1−3 leaves (Tunheim et al., 2019).

In this study, we carried out experiments on nests containing spotted-white eggs (Figure 1A). The mean weight, length, and width of the common tailorbird eggs were 0.92±0.01 g, 15.50±0.07 mm, and 11.09±0.06 mm (mean±*SD*, same below; *n*=38), respectively. Real white eggs (Figure 1B) were purchased from munia (*Lonchura* spp.) suppliers with mean weight, length, and width of 1.03± 0.02 g, 16.60±0.32 mm, and 12.36±0.29 mm (*n*=20), respectively. Blue and white soft clays were manually molded into model eggs before they were baked for setting and were similar in size and shape to the common tailorbird eggs (Figure 1C, D). The mean weight, length, and width of the model eggs were 1.56±0.01 g, 15.79±0.16 mm, and 11.46±0.08 mm (*n*=15) respectively.

We followed the methods of Yang et al. (2015a) to carry out egg rejection tests during the early stage of incubation. All experimental nests were independent and not parasitized. The experiments were carried out during the breeding season and were randomly performed. Four experimental groups were used: (1) real white eggs were added to 31 common tailorbird nests to test recognition ability. These eggs differed from common tailorbird eggs in that they were immaculate; (2) blue model eggs that differed greatly in color were added to 12 nests and (3) white model eggs that were similar in background color but without spots were added to 12 nests to test if the birds were able to recognize these as foreign eggs; (4) one blue model egg and one real white egg (Figure 1E) were added to 16 nests to examine the effects of nest sanitation on egg rejection behavior. Videos were then used to record the egg rejection behavior of the common tailorbirds. The experimental period was 6 d, and the study either ended when rejection occurred or after 6 d. Nests were monitored every 1−2 d for evidence of egg ejection and removal of model eggs (Yang et al., 2015a, 2019).

Data analysis was performed using IBM SPSS 25.0 software (IBM Corp., Armonk, NY, USA). Fisher's exact test was used to compare the probability of rejecting real white

eggs in different experimental groups. All tests were two-tailed, and the significance level was $P<0.05$. All data are presented as mean±SD.

The experiments reported here comply with the current laws of China. All animal procedures performed in this research were in accordance with the ethical standards of the Animal Research Ethics Committee of Hainan Provincial Education Centre for Ecology and Environment, Hainan Normal University (permit no. HNECEE-2012-002).

The common tailorbirds generally used their bills to remove the model and real eggs. Of the 31 nests in the first group, real white eggs were rejected from only five nests (16.1%). In the second and third groups, the blue and white model eggs were rejected from all 12 nests (100%), respectively (Table 1). In the fourth group, however, although the blue model eggs were rejected from all 16 nests (100%), the real white eggs were rejected from only eight nests (50.0%) (Table 1). Differences were observed in the time taken to reject real eggs (from $1-4$ d) and model eggs (within 5 h after parasitism). When both real eggs and blue model eggs were added, the bird rejected the blue model egg before the real egg. No differences were observed between nests with the addition of white model eggs and blue model eggs (100% ejection in both cases). However, there was a highly significant difference in the rejection rates between nests with only real white eggs and nests with white or blue model eggs added (χ^2=38.176, df=2, $P<0.001$). There was also a significant difference in the rejection rates between nests with only real white eggs and nests with both real eggs and blue model eggs (χ^2=6.051, df=1, P=0.02), i.e., the addition of blue model eggs increased the rejection rate of real white eggs from 16.1% to 50%.

Table 1 Number of nests in which a model egg was rejected (% total nests) and number of nests in which a real white egg was rejected (% total nests)

Experimental group	Model egg rejection (%)	Egg rejection (%)	Number of nests tested
One real white egg	–	5 (16.1)	31
One blue model egg	12 (100)	–	12
One white model egg	12 (100)	–	12
One blue model egg and one real white egg	16 (100)	8 (50.0)	16

–: Not available.

Egg rejection by hosts remains one of the most striking examples in nature of how discrimination in social behavior evolves (Gloag & Beekman, 2019). Our results showed that common tailorbirds possessed strong nest sanitation ability, and that nest sanitation behavior directly affected egg recognition of real white eggs. Therefore, nest sanitation behavior increased the probability of foreign egg rejection. The rate at which common tailorbirds reject real mimetic white eggs was previously reported to be low (Yang et al., 2016). However, Yang et al. (2016) used conspecific white eggs with spots, whereas we used white eggs without spots. In our study, the recognition and rejection of 100% of the white and blue model eggs by the common tailorbirds demonstrated strong nest sanitation and egg recognition abilities. Interestingly, when both blue model eggs and real white eggs were added to a nest, the proportion of real white eggs rejected increased significantly, suggesting that rejection of blue model eggs elicited egg rejection behavior in these cuckoo hosts. We also found that the tailorbirds rejected the blue model eggs before they rejected the real white eggs.

Previous studies on nest sanitation and egg rejection behavior have suggested that a host's egg recognition ability is an extension of its nest sanitation behavior (Gigueno & Sealy, 2009, 2017; Moskát et al., 2003; Yang et al., 2015a, 2015b). Yang et al. (2015a) studied the relationship between nest sanitation and egg rejection in barn swallows, a host of common cuckoos, and found that the addition of peanut shells alongside model eggs significantly increased the probability of the model eggs being rejected compared to nests in which only model eggs were added. This suggests that nest sanitation behavior in hosts can significantly affect egg recognition. In our study, common tailorbirds rapidly rejected 100% of the egg-shaped blue model and white model eggs added to their nests. These model eggs had the same effect as peanut shells in Yang et al. (2015a).

The rejection of all model eggs suggests a ubiquitous cleaning method and further implies that common tailorbirds have a strong ability to recognize and exclude egg-shaped objects similar in size to their own, which is consistent with the second stage of recognition of egg-shaped objects mentioned by Moskát et al. (2003). When the blue model egg was added alongside the real white egg, rejection ability increased because the sudden appearance of an obvious foreign object stimulated nest sanitation behavior. This resulted in the tailorbirds paying greater attention to other objects in the nest, i. e., their egg recognition ability was also activated, thereby increasing the egg rejection rate.

Common tailorbird nests are leaf-shaped and similar to cavity nests. During the hatching stage, foreign objects can fall into such nests. In addition, common tailorbirds are hosts to plaintive cuckoos and experience high cuckoo parasitism pressure (Nahid et al., 2016; Tunheim et al., 2019). Undoubtedly, parasitic eggs are major foreign objects in their nests. At the same time, plaintive cuckoos and common tailorbirds both produce spotted-white or spotted-blue eggs. However, when plaintive cuckoos parasitize the nests of common tailorbirds, the color of their eggs does not exactly match that of the host's (Yang et al., 2016). This difference in color between the parasitic and host eggs significantly increases the probability of egg rejection. In this sense, egg
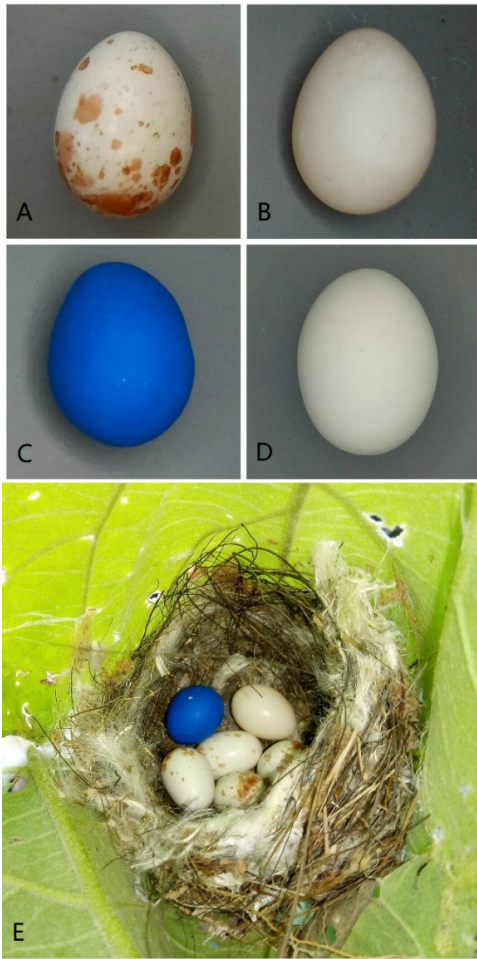
Figure 1 Photographs of common tailorbird egg (A), real white egg (B), blue model egg (C), white model egg (D), and example of experimental group with addition of one real white egg and one blue model egg (E) (Photos by Chang-Zhang Feng)

recognition is promoted in common tailorbirds through the presence of parasitic eggs that are recognizably different in color (Yang et al., 2016). This is similar to the removal of egg-shaped objects that differ from host eggs during nest sanitation behavior. However, the difference lies in egg color (Moskát et al., 2003). Common tailorbirds reject blue model eggs before rejecting real white eggs. This suggests that nest sanitation behavior evolved before egg recognition. In addition, egg rejection behavior in common tailorbirds toward model eggs and real white eggs is similar. This shows that egg rejection behavior is an extension of nest sanitation behavior. After blue model eggs were added, nest sanitation behavior was strengthened while the ability to reject real white eggs also increased.

Differences in egg recognition abilities are found among different bird species and populations, which explains why some previous studies found no relationship between nest sanitation and egg rejection. For example, the addition of foreign objects had no effect on the rejection rate of foreign eggs in red-winged blackbirds, an egg accepter of cowbirds (Kemal & Rothstein, 1988; McMaster & Sealy, 1997; Peer, 2017). Furthermore, the addition of peanut shells to brown-breasted bulbul nests (an egg rejecter) had no effect on the rejection of model eggs (Su et al., 2018). However, Yang et al. (2015a) found that the addition of peanut shells to barn swallow nests improved the rejection rate of model eggs. Common tailorbirds can recognize foreign eggs without stimulation of nest sanitation behavior, but the addition of obvious foreign objects may increase its motivation to recognize eggs in the nest and time spent checking. Evidently, more studies on the relationship between host nest sanitation behavior and egg rejection abilities are required to explain the origin of egg rejection ability.

The experiments carried out in the present study showed no significant differences between artificial model eggs and real eggs. This agrees with the results of Peer et al. (2002), who placed model eggs and brown-headed cowbird (*Molothrus ater*) eggs into northern mockingbird (*Mimus polyglottos*) nests and found no differences in the rates at which real eggs and model eggs were rejected. Guigueno & Sealy (2012) also determined that the shape and size of model eggs are important factors in host rejection of non-egg-shaped objects. Here, common tailorbirds rejected 100% of non-mimetic white model eggs added to their nest, but accepted some mimetic real white eggs, indicating that these birds can distinguish between white model and real eggs. This also suggests that more attention should be paid to bias in birds with strong egg recognition abilities (e.g., Yang et al., 2019) when model eggs are used to test host egg recognition in brood parasitism studies. In addition, understanding the phylogenetic distribution and transitions of nest sanitation and egg rejection behavior should facilitate future research (Liang et al., 2013).

In conclusion, our study showed that common tailorbirds possessed strong nest sanitation and recognition abilities and used their bills to remove model eggs similar in shape and size to their own. In addition, we demonstrated that the removal of egg-shaped foreign objects (e. g., model eggs) directly improved the birds' egg recognition ability. The association between egg ejection and nest sanitation in common tailorbirds provides valuable information on the cognitive decision-making processes of this plaintive cuckoo host. Furthermore, our study suggests that egg recognition ability in birds likely evolved from nest sanitation behavior and that egg recognition is a more advanced form of nest sanitation behavior.

COMPETING INTERESTS

The authors declare that they have no competing interests.

AUTHORS' CONTRIBUTIONS

W.L. designed the study; C.F. carried out field experiments; C.Y. performed laboratory and statistical analyses. C.F. wrote the draft manuscript; W.L. helped improve the manuscript. All authors read and approved the final

version of the manuscript.

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