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Letter to Editor

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Attractive egg color? Red eggs facilitate egg acceptance in a cavity-nesting host

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Hosts evolve defensive strategies to minimize the reproductive costs of brood parasitism, in turn, the hosts' defense promote the optimization of cuckoo parasitism strategies (Soler 2017). Recognizing foreign eggs and selectively removing them from the nest can minimize the fitness costs associated with rearing parasitic fledglings (Soler 2017). Since Rothstein (1971) first experimented with the addition of a model egg to a host nest in the early incubation period to study host egg recognition, the use of model eggs has become one of the most important methods for testing the egg recognition abilities of hosts (Hauber et al. 2019). Some studies have looked at various egg colors and their effect on host egg rejection and found differential responses to egg colors (for more details, see Supplementary Materials), highlighting that more work needs to examine the effect of model egg color on host egg rejection behavior. Previous work showed that southern Kuankuoshui populations of green-backed tits (*Parus monticolus*) possess high egg recognition abilities and exhibit relatively high egg rejection rates for non-mimetic light blue eggs (Yang et al. 2019). Kuankuoshui is located in Guizhou, southwestern China, and Liupanshan is located in Ningxia, northwestern China. The distance between the two locations is about 800 km as the crow flies. Due to differences in the history of co-evolution and reciprocal pressure, even different geographic populations of the same host can exhibit significant geographic variation in the recognition and rejection of foreign eggs. Nevertheless, it is not known whether green-backed tits from northern Liupanshan populations that lack a co-evolutionary relationship with cuckoos possess egg recognition abilities, and whether the base colour of the non-mimetic model affects egg rejection behavior in this cavity-nesting host. If so, are red eggs more attractive to green-backed tits? The main purpose of this study was to determine the role of non-mimetic model background color in egg recognition in green-backed tits. We would expect that the Liupanshan population of green-backed tits also have high egg recognition ability and similar rejection rates for non-mimetic eggs of different colors.

During the 2021 and 2022 breeding seasons, nests of green-backed tits that were in the early incubation period were subjected to the following model egg parasitism experimental treatments: group 1, where one blue model egg was added directly to each nest (n = 48); group 2, where one red model egg was added directly to each nest (n = 30), and group 3, a control group in which nests were visited with the same procedure without experimental eggs to control for human disturbance (n = 16). The experimental nests were examined on the second day, followed by re-examination on day 6 (see Supplementary Materials). In the control group, we did not find the occurrence of rejection or abandonment. Our results indicated that the Liupanshan population of green-backed tits also possessed relatively high egg recognition abilities, with a rejection rate of 93.8% for blue model eggs and 60% for red model eggs, where a significant difference exists between the rejection rates of eggs from both models (Pearson's chi-squared test, x^2 = 13.539, df = 1, P = 0.0002; Figure 1). We showed that the northern population of Liupanshan green-backed tits have a relatively high egg recognition ability compared with other southern populations of the same species (Table 1), which is consistent with what we expected. However, we observed that green-backed tits were found to have a significantly higher rejection rate for blue model eggs compared to red model eggs, contrary to our expectations.

The results of the present study suggest that the color of model eggs influences host egg rejection behavior, even when both are non-mimetic model eggs to the green-backed tit. Higuchi (1989) tested the egg recognition ability of Japanese bush warblers *Cettia diphone* using six different colored model eggs and attributed the acceptance of chocolate brown and red egg to the fact that these colors were closer to the egg color spectrum of the warbler host. However, such an explanation (mimicry) cannot account for the high acceptance rates of rufous bush chat *Cercotrichas gulactotes* for two non-mimetic model eggs (non-mimetic plain white and white with black spots) (rejection rates < 20% for both; Alvarez 1999). The green-backed tits we studied laid eggs of white

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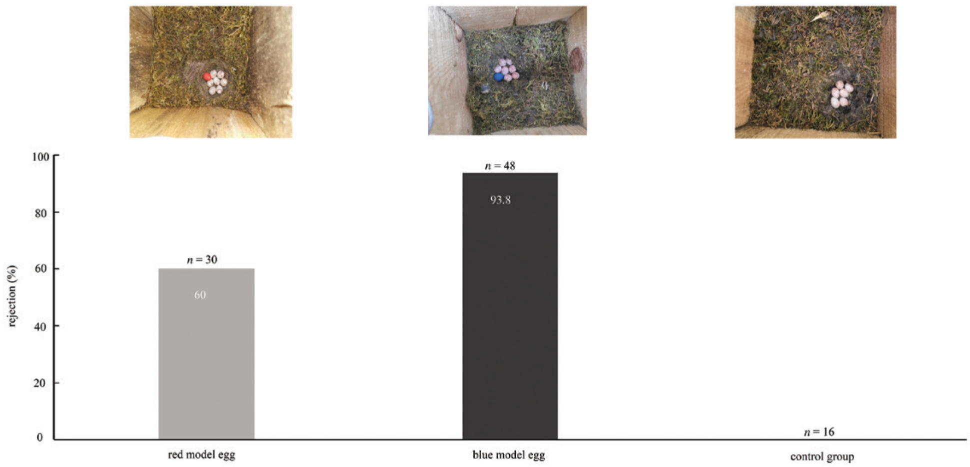

Figure 1. Egg rejection rate of the Liupanshan population of green-backed tits. Numbers in bars refer to the percentages of egg rejection.

Table 1. Rejection frequencies of experimental eggs among different geographical populations of green-backed tits in China.

Study site	Species	Treatment	Nests tested (*n*)	Rejection rate (%)	Reference
Kuankuoshui, Guizhou	Green-backed tit	Own egg painting blue	20	100	Yang et al (2022)
Kuankuoshui, Guizhou	Green-backed tit	Blue model egg	28	100	Yang et al. (2019)
Aowanda, Taiwan	Green-backed tit	Blue model egg	12	75	Liu et al. (2020)
Kuankuoshui, Guizhou	Green-backed tit	Blue model egg	12	100	Liu et al. (2020)
Liupanshan, Ningxia	Green-backed tit	Blue model egg	48	93.8	This study
Liupanshan, Ningxia	Green-backed tit	Red model egg	30	60	This study

background color with reddish-brown spots (Yang et al. 2019). Both blue and red model eggs appear to be non-mimetic model eggs to the human eye, and the rejection rates of both non-mimetic model eggs by green-backed tits are similarly very high, in line with expectations that hosts with high egg recognition ability will reject non-mimetic model eggs at a high rate (Cassey et al. 2008). Birds have 4–5 types of single cone photoreceptors, including one type sensitive to UV light (for comparison humans have only three types of cone photoreceptors), so the perception of colors by birds may differ from that of humans, which may also cause green-backed tits to respond differently to the two different colors of model eggs. According to the multiple threshold decision rule, the response of host to alien eggs is based on absolute perceivable differences between a foreign egg and a host's own egg color, and there is an acceptance range for the degree of absolute perceivable differences between a foreign egg and a host's own egg color (Hanley et al. 2017). We did not measure the magnitude of the absolute perceivable difference values between the egg colors of green-backed tits and longer wavelengths of red and shorter wavelengths of blue. Therefore, it cannot be ruled out that the absolute perceptible difference values for blue, red and green-backed tit egg colors are different. The larger the absolute difference value, the more likely it is to be rejected (Cassey et al. 2008), thus possibly accounting for the higher rejection rate of blue model eggs compared to red model eggs by green-backed tits. Some birds may not able to detect differences among egg colorations in dim hole-nests (Avilés et al. 2011; but see Yang et al. 2022). It is also possible that green-backed tits have trouble discriminating red (but not blue) colors in the low light conditions of their nest boxes, potentially due to birds have better vision at low (UV-Blue) than at high (red) wavelengths, blue eggs with shorter reflective wavelengths were more likely to be detected by birds than red eggs with longer reflective wavelengths in dim environments. Future work should investigate how these colors appear to the birds in dark light. The single threshold decision rule theorizes that differences in directional egg coloration may better explain the egg rejection behavior of the host (Hanley et al. 2017). For example, some studies have shown that hosts will reject eggs that are significantly browner than their own egg colour and accept eggs that are significantly bluer than their own egg color (Hanley et al. 2017), regardless of the magnitude of the absolute perceptible difference value between the bluer eggs and their own egg color. In our study, despite significant differences in rejection rates between red and blue model eggs, green-backed tits had very high rejection rates for both types of eggs, which may not support the single threshold decision rule theory. The perception of a particular color may influence the bird's egg rejection response (Cassey et al. 2008), thus it may also be the case that red may act as a superstimulus for them (a supernormal or red egg is attractive; Alvarez 1999), or they have an innate aversion to blue, which accounts for the significant differences in rejection rates between the two color model eggs and requires further study. To sum up, our study provided the experimental evidence that even for non-mimetic model eggs, the color of model eggs can have an important effect on egg recognition in a cavity-nesting host. If the preference for certain visual stimuli (e.g., red eggs) by the host was the main selective force in the process of attaining egg acceptance, parasitic cuckoos would evolve the type of egg coloration that may be preferred and accepted by the host rather than that is similar to the host's egg coloration. This would open up new avenues to discover the evolution of cuckoo egg mimicry, which need to be verified in more host species.

Ethical standards

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 (No. HNECEE-2014-005).

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Authors' contributions

WL designed the study, XW and JL carried out field experiments, JL performed the analyses and wrote the draft manuscript, WL edited and improved the manuscript. All authors approved the final submission.

Conflict of interests

The authors declare that they have no competing interests.

Supplementary Materials

Supplementary materials (Materials and methods, and Table S1) can be found at https://academic.oup.com/cz.

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