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ORIGINAL PAPER

# Cryptic eggs are rejected less frequently by a cuckoo host

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## Abstract

Obligate brood parasitism is associated with huge reproduction costs, forcing hosts to evolve various anti-parasitic strategies against brood parasites, among which egg recognition and rejection is the most effective defense strategy. According to the crypsis hypothesis, non-mimetic yet cryptic eggs in a nest can also deceive their hosts and eventually be accepted. To validate this hypothesis, we conducted field experiments on Oriental reed warblers (*Acrocephalus orientalis*), a common host for common cuckoos (*Cuculus canorus*). We firstly tested the egg recognition and rejection abilities of Oriental reed warblers, using black and white model eggs in natural nests. Then we designed a comparison test where the cryptic effects of the two groups of experimental eggs were different. We manipulated the nest lining color and added relatively cryptic and bright model eggs to test warblers' rejection behaviors against cryptic and bright foreign eggs. The results showed that warblers have strong egg recognition and rejection abilities. There is a significant tendency for warblers to prefer to peck and reject relatively distinguishable foreign eggs, which supports the crypsis hypothesis. These findings indicate that even in the host-parasite system of open nests, parasitic eggs that are cryptic enough are prevented from being discovered and rejected by the host, and thus obtain the possibility of successful parasitism.

**Keywords** Common cuckoo · Egg crypsis · Egg removal · Egg recognition · Oriental reed warbler

## Introduction

Avian obligate brood parasites lay eggs in other birds' nests, which results in reproduction costs to their hosts. The cost of parasitism is high for the host (Lyu and Liang 2021) because parasites will remove or destroy host eggs during the parasitic process (Davies 2000); the exclusive parasitic nestling, after hatching, will remove all other host eggs or host nestlings in the same nest (Davies 2011; Soler 2014), or the non-exclusive parasitic nestling will win the competition for food (Davies et al. 1998; Kilner 2003); and compared to the host's own nestlings, they require more time and energy from the host (Rothstein 1990; Feeney et al. 2014; but see Samaš et al. 2018, 2019). The pressure exerted by such high costs forces the host to evolve abilities to recognize and reject parasitic eggs or to take defensive actions such as guarding against and attacking parasites (Davies and Brooke 1989; Soler et al. 1999; Røskaft et al. 2002; Avilés et al. 2004; Moskát 2005). Recognizing and rejecting parasitic eggs, compared to other defensive strategies, is an effective anti-parasitic strategy when parasitism happens because it is time- and effort-saving, and avoids direct confrontation

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with parasitic birds (Davies and Brooke 1989; Moksnes et al. 1991, 2013; Sealy and Underwood 2012).

It is highly likely for non-mimetic eggs to be recognized and rejected by the host. For their eggs to be accepted by the host, some parasites have evolved to lay eggs that highly match their host's eggs in appearance. For example, egg mimicry by common cuckoos (*Cuculus canorus*) occurs in some warbler hosts (Avilés et al. 2006; Cherry et al. 2007; Honza et al. 2014; Li et al. 2016). Furthermore, plaintive cuckoo (*Cacomantis merulinus*) eggs laid in common tailorbird (*Orthotomus sutorius*) nests (Yang et al. 2016a, b) and Oriental cuckoo (*Cuculus optatus*) eggs laid in yellow-bellied prinia (*Prinia flavientris*) nests (Wang et al. 2015) are both highly mimetic.

For species without egg color mimicry, an alternative strategy would be to lay eggs with cryptic colors. Such eggs are more likely to be overlooked by the host, being less distinguishable in the nest due to low surface brightness, and thus more likely to eventually achieve successful parasitism. This approach apparently possesses similarities with egg mimicry, e.g., several species of Australasian bronze-cuckoos (*Chalcites* spp.) and their common hosts *Gerygone* and *Acanthiza* spp. (Langmore et al. 2009; Gloag et al. 2014), and the shining bronze-cuckoo (*Chalcites lucidus*) with their sole host the grey gerygone (*Gerygone igata*) in New Zealand (Thorogood et al. 2017).

It is most suitable to test the egg crypsis hypothesis in darker nests such as the nests of the large-billed gerygone (*Gerygone magnirostris*) (Gloag et al. 2014), yellow-rumped thornbill (*Acanthiza chrsyorrhoa*) (Medina and Langmore 2019) and common redstart (*Phoenicurus phoenicurus*) (Samaš et al. 2016). Unfortunately, these hosts are egg acceptors, and they rarely recognize and reject foreign eggs, including model eggs and parasitic cuckoo eggs. Even when the brightness of the nest is manually increased so that the host is able to clearly see the foreign eggs in the nest, the egg rejection rate does not increase, indicating that a rapid increase of visibility in the nest does not change the host's rejection behaviors (Avilés et al. 2015; Medina and Langmore 2019). Yang et al. (2016a, b) investigated egg mimicry in common cuckoos, parasites of Oriental reed warblers (*Acrocephalus orientalis*, hereafter "warblers"), in China using spectrum analysis to analyze similarities in cuckoo and warbler egg color and pattern. The results showed that the cuckoo eggs were not as fully mimetic as the host eggs. Some cuckoo eggs were greyer on the surface (Fig. 1a), with a higher surface brightness than that of the host eggs (Fig. 1b). Although these eggs were dissimilar to the host eggs, they were accepted and hatched anyway. From this point, it seems that cryptic eggs in open nests can also be deceptive to a certain extent. To understand whether cryptic foreign eggs can deceive hosts in the parasitic system of open nests, we conducted a test on the ability of warblers to recognize and reject foreign eggs. We simultaneously devised an experiment with two groups, one with more cryptic model eggs and the other with brighter model eggs, to observe the rejection behaviors of the warblers. According to the egg crypsis hypothesis, we predicted that if the warblers had strong egg recognition ability, they would preferentially reject more distinguishable foreign eggs.

## Materials and methods

### Study area and study species

We performed this study at the Zhalong National Nature Reserve (46°48′–47°31′N, 123°51′–124°37′E) in Heilongjiang, northeastern China. Field experiments were conducted during the breeding season (June to August) between 2012 and 2019. We systematically searched for Oriental reed warbler nests in reed swamps in our study area and identified

**Fig. 1** Eggs of the common cuckoo and Oriental reed warbler in the nests (**a** shows single parasitism with one cuckoo egg and **b** shows the multiple parasitism case. The *yellow arrow* pointed eggs are cuckoo eggs)

nests parasitized by the common cuckoo (Wang et al. 2020a, b). The parasitism rate ranged from 34.3% to 65.5% in our study area (Liang et al. 2014; Yang et al. 2014).

## Field experiments

We numbered each warbler nest discovered in the field and recorded the dates, clutch size, and cuckoo parasitism. In the incubation stage (usually after four eggs were laid), we performed the following three sets of experiments to test the warblers' abilities to recognize and reject different foreign eggs: (1) the black model egg trial, where we inserted one black model egg made of synthetic clay into the natural warbler nest (egg length: 22.71 ± 0.63 mm, egg width: 17.47 ± 0.49 mm, egg mass: 3.56 ± 0.31 g, mean ± SD; $n = 15$); (2) the white model egg trial, where we inserted one white model egg made of synthetic clay into the nest (22.56 ± 0.82 mm, 17.06 ± 0.83 mm; egg mass: 3.47 ± 0.28 g; $n = 15$); (3) the common cuckoo egg trial, where we recorded natural cuckoo parasitism and cuckoo egg rejection by the host from years 2012–2019 (22.41 ± 0.88 mm, 17.08 ± 0.56 mm; egg mass: 3.74 ± 0.29 g; $n = 15$).

In addition to the above egg recognition experiment, we further examined the warblers' rejection behaviors toward foreign eggs with a cryptic color and with a bright color. To minimize the influence on the reproduction of the warblers, we set up an experimental nest at a spot 0.5 m away from the focal warbler nest. We found this distance was suitable for our experimental design, as the warblers would visit experimental nests quickly and then reject the model eggs, perhaps the alien nests may have encroached on their breeding territory. The experimental nests were natural nests collected during the previous breeding season. Two experimental groups were set up. In group 1, the inside of the nest was painted with black spray paint (Fig. 2, group 1), and the nest was dried and left for more than a week before being used for the experiment to ensure there was no smell. Two black model eggs and two white model eggs were placed in the nest (egg length = 17.68 ± 0.42 mm, egg width = 13.40 ± 0.31 mm, and egg mass = 2.76 ± 0.27 g; $n = 15$). The set-up of this group was to highlight that the white model eggs were more distinguishable while the black eggs were more cryptic against a black nest lining. The warblers would visit the experimental nest, and then recognize and reject the eggs in it. We predicted that the warblers would first reject the white eggs.

On the contrary, the set-up of group 2 was designed to help black cryptic eggs become more distinguishable and bright white eggs become more cryptic. We painted the nest lining white following the same methods as for group 1 and placed the same set of black and white model eggs within it (Fig. 2, group 2). We predicted that the warblers would first reject black eggs: the opposite result to that observed in group 1.

To determine the levels of concealment of the eggs placed in the black and white nests, we measured the color

**Fig. 2** Example of experimental nests and active Oriental reed warbler nests in the field. Group 1 refers to the painted black color nest lining, and the white nest lining in group 2

difference between the experimental eggs and the nest lining. A Canon EOS 20D camera was used to take photos of the experimental nests. Birds can detect ultraviolet (UV) light besides visible light by using the fourth cone cell type in the retina (Bennett et al. 1996; Cuthill et al. 2000; Rajchard 2009; Šulc et al. 2016), however, in this study, all model eggs were made of synthetic clay, which have no UV reflectance spectra (300–400 nm) on egg appearance (i.e., Gloag et al. 2014; Yang et al. 2019), in this case, cuckoo cannot remove the model egg depend on the UV cue. Therefore, we try to use the method of CIE$L^*a^*b^*$ to quantify the degree of crypsis of the eggs in the black and white nests (Robertson 2007; McCormick-Goodhart and Wilhelm 2003).

We used the CIE $L^*a^*b^*$ (International Commission on Illumination) color space in Adobe Photoshop CS6 (Robertson 2007; McCormick-Goodhart and Wilhelm 2003) to measure the colors of the nest lining and the eggs. The $L^*$ value represents brightness while $a^*$ and $b^*$ indicate chromaticity, with values representing the color ranges of red to green, and yellow to blue, respectively. For the measurement of egg colors, we took the entire photo to obtain all the parameters of the egg; as for the value of the nest background color, we took four squares of the same size around the egg to measure and calculate the average (Wang et al. 2021; Xiao et al. 2016). After the values of $L^*$, $a^*$ and $b^*$ were obtained, we used an equation to calculate the overall color difference ($\Delta E$) between the eggs and the nest lining, using the calculation result to indicate the cryptic level or the distinguishable level. The equation for calculating the overall color difference ($\Delta E$) is as follows:

$$\Delta E=\sqrt{\left(L_{\mathrm{m}}^{*}-L_{\mathrm{n}}^{*}\right)^{2}+\left(a_{\mathrm{m}}^{*}-a_{\mathrm{n}}^{*}\right)^{2}+\left(b_{\mathrm{m}}^{*}-b_{\mathrm{n}}^{*}\right)^{2}}$$

where m stands for model egg and n for nest lining. The lower the $\Delta E$, the more cryptic the model egg in the nest. On the contrary, the higher the $\Delta E$, the more distinguishable the model egg. In the end, 15 photos were selected for the black nest and the white nest, respectively, recording a total of 30 black and 30 white model eggs.

All the experimental nests were checked daily to assess the warbler response after five days (Moksnes et al. 1991; Wang et al. 2015; Medina and Langmore 2019). The warbler's response was classified as rejection or acceptance. If the model egg disappeared during the observation period, the egg was considered to have been rejected. If the model egg remained undamaged and the clutches remained actively incubated by the sixth day, it was deemed to be accepted. There was no interference from the experimenters towards the warblers during the experimental process.

### Statistical analysis

Binomial tests (two-tailed test) were used to analyze the frequency of warblers rejecting cryptic model eggs in relation to non-cryptic model eggs. One-way ANOVA was used to test for color differences ($\Delta E$) between the nest linings and the model eggs. Differences were considered to be significant at $p<0.05$, highly significant at $p<0.01$, and not significant at $p>0.05$. Statistical analysis was conducted using IBM SPSS Version 25.0 (IBM Corp., Armonk, NY, USA).

**Table 1** Egg rejection in Oriental reed warblers to model eggs (black and white color) and naturally parasitized cuckoo eggs

| Egg type | Rejection (%) | Acceptance | Sample size |
|---|---|---|---|
| Black model egg | 15 (100) | 0 | 15 |
| White model egg | 24 (100) | 0 | 24 |
| Common cuckoo egg | 13 (4.3) | 289 | 302 |

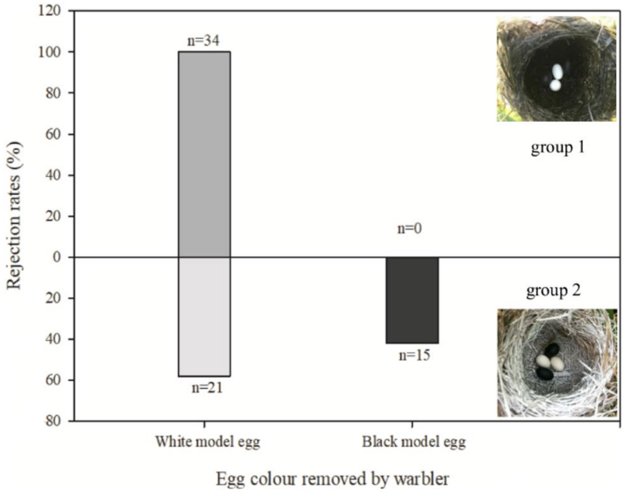

**Fig. 3** Rejection frequency of Oriental reed warblers choosing experimental eggs in relation to the different color of model eggs in *black* nest lining (group 1) and *white* nest lining (group 2). Numbers above the bars refer to sample size

## Results

Not only were warblers able to recognize and reject 100% of the model eggs (Table 1), they were also able to reject some of the naturally parasitic cuckoo eggs (4.3%, 13 out of 302). Warblers showed a significant egg rejection response toward white model eggs versus black model eggs in a black nest lining (Binomial test, $p<0.0001$, Fig. 3, group 1). However, no difference in egg rejection was seen in response to black and white model eggs in a white nest lining (Binomial test $p=0.405$, Fig. 3, group 2).

The mean color difference ($\Delta E$) between the black nest lining (Table 2) and the white model egg was 207, while the mean $\Delta E$ between the black nest lining and the black model egg was 25. This was a significant difference, indicating that black model eggs are highly significantly cryptic

**Table 2** Color difference ($\Delta E$) between white and black model eggs in artificial painted nest lining ($N$ refers to nest sample size)

| Nest color | $\Delta E$ | | $N$ | $F$ | df | $p$ |
|---|---|---|---|---|---|---|
| | White model egg | Black model egg | | | | |
| Black nest lining | 207.36 ± 12.78 | 25.81 ± 7.19 | 15 | 2298.514 | 1 | $< 0.001$ |
| White nest lining | 69.19 ± 7.84 | 78.76 ± 18.96 | 15 | 3.273 | 1 | 0.081 |

compared to white ones in a black nest lining ($F = 2298.514$, $p < 0.001$). Conversely, mean $\Delta E$ between the white nest lining (Table 2) and the white model egg was 69, while the mean $\Delta E$ between the white nest lining and the black model egg was 78. There was no significant difference in $\Delta E$ between the two colors of model eggs, indicating that there is no significant difference in crypsis between the two egg colors in a nest with white lining ($F = 3.273$, $p = 0.081$).

Additionally, our video-recordings showed that warblers first removed the white model egg in the black nest lining in group 1 (ESM Video S1). However, in group 2, warblers either first removed both the white and the black model eggs (ESM Video S2 and S3).

## Discussion

We tested warblers' abilities to recognize and reject non-mimetic model eggs and further examined their rejection behaviors toward the different cryptic model eggs placed against the black nest lining and the white nest lining. The results showed that warblers were able to recognize and reject all non-mimetic model eggs and a few of the naturally parasitic mimetic cuckoo eggs. Consequently, cuckoos must evolve more mimetic or cryptic eggs to be better accepted by the hosts. In the cryptically colored egg experiment, the warblers rejected almost the white model eggs against the black nest lining, which was in line with our prediction. However, in the group with black model eggs against the white nest lining, the result did not support our hypothesis. In general, during our observations, warblers chose to reject brighter foreign eggs while the eggs with the more cryptic color could be kept and accepted.

In other host species, it has been observed that some natural parasitic eggs will also be rejected. For example, eastern olivaceous warblers (*Iduna pallida elaeica*) were observed to reject 12% of common cuckoo eggs (Antonov et al. 2007). Similarly, great reed warblers (*Acrocephalus arundinace*) rejected 57% of cuckoo eggs (66 out of 116) by ejection ($n = 45$), desertion ($n = 20$), or by egg burial with nest material ($n = 1$) (Trnka et al. 2012). In the present study, the rejection rate of cuckoo eggs was 4.3% (13 out of 302). The rejection rate may have been underestimated due to hosts possibly having rejected parasitic eggs prior to being discovered (Davies 2000; Samaš et al. 2014; Li et al. 2016). We observed that accepted eggs tended to be more mimetic or cryptic (i.e., Fig. 1a). From this point of view, producing cryptic eggs is adaptive for parasitic cuckoos. First, it can maximize the possibility of its eggs not being recognized and rejected by the host, and second, it can also prevent a second cuckoo female from removing its eggs in a multi-parasite nest (Gloag et al. 2014). When a mimetic parasitic egg and a host egg are in the nest together, the probability of them being caught by a parasite is identical. However, a cryptic egg is less likely to be detected, achieving a lower probability of being recognized and removed (Wang et al. 2021). Therefore, from a comprehensive point of view, eggs with cryptic colors are more advantageous.

Laying relatively more cryptic eggs may prevent subsequent female cuckoos from noticing the egg during the limited time of the parasitism process. For example, the olive-brown eggs laid by Australian bronze-cuckoos that are cryptic, yet far from being similar to their host eggs, still managed to be accepted by the hosts (Langmore et al. 2009; Gloag et al. 2014), indicating that cryptic eggs are more difficult to be detected. Therefore, in group 1 of our experiment, the color of the black model eggs was almost identical to that of their nest lining, making them highly cryptic. By contrast, the white eggs in the same nest lining stood out and were rejected by the warblers. The results proved to be a good interpretation of the crypsis hypothesis.

Our findings are not consistent with previous work showing that increased egg-nest visual contrasts do not increase parasitic egg discriminability and rejection in hosts eastern phoebes (*Sayornis phoebe*) and American robins (*Turdus migratorius*) of brown-headed cowbirds (*Molothrus ater*). They found that despite successfully increasing egg-nest visual contrast in their treatments, these two hosts did not increase the rate of reject model parasitic eggs (Aidala et al. 2015, 2019). In great reed warblers (*Acrocephalus arundinaceus*) of common cuckoos, egg-nest contrast was a collateral, not a causal factor in egg rejection (Hauber et al. 2015). It is possible that their treatment reciprocally dyed both eggs and the nest lining with one of two colors: orange and green, and the contrast is not distinct compared with our study: the black and white color are more distinct.

In the white nest lining in group 2, we predicted that the white model eggs should be more cryptic, and the black ones more distinguishable and therefore possibly more likely to be carried off by the warblers. However, the results were not consistent with this prediction. The warblers randomly rejected the model eggs in the nest, and there was no significant difference in rejection between black and white eggs, as there was in group 1. To our surprise, the number of white model eggs picked was slightly higher than the number of black eggs. Some possible explanations are as follows.

Firstly, in the white nest lining, the crypsis of the white model eggs did not achieve our expected level, where its $\Delta E$ showed no significant difference, just like that of the black model eggs. As a result, both colors were distinguishable, resulting in similar removal rates. Alternatively, the white spray paint cannot make the nest lining look obviously different in color, therefore, white or black model eggs look no different together within a nest.

Second, in nature, bird eggs are mostly white, blue, and brown, and there are few reports of pure black bird eggs (Kilner 2006). The egg color of this warbler species, and of its host species, common cuckoos, is white (Liang et al. 2014; Li et al. 2016; Yang et al. 2016a, b). It is likely that warblers are more sensitive to white eggs and as a result, the white model eggs were removed first in this experiment.

Finally, in the field, we found that when a small number of warblers lay their last egg, it may be pure pale or lighter coloration in egg appearance, e.g., the eggshell has no black spots, which is a relatively common phenomenon in most birds (Ruxton et al. 2001; Peer and Sealy 2004; Kilner 2006; Huo et al. 2018). Therefore, white eggs may be more likely to be considered as threatening foreign parasitic eggs by warblers, and therefore to be preferentially removed.

In conclusion, the results of the present study support the crypsis hypothesis, revealing that even in open nests, more distinguishable eggs are preferentially removed by the host while more cryptic eggs are spared and kept. This allows us to further understand why parasites choose to lay eggs that are either more mimetic to the host eggs or more cryptic. The advantage of doing so is to better increase the chance of the eggs being accepted by the host. We validated the crypsis hypothesis by conducting experiments on how host birds remove eggs. However, whether a natural parasitic egg that carries cryptic features, but is not mimetic at all to the host eggs in terms of color, can deceive the host in an open nest with relatively good lighting conditions still requires further study.

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**Authors' contributions** W.L. designed the study; L.W., J.M. and Y.Z. carried out field experiments; L.W. performed statistical analyses and wrote the draft manuscript; W.L. improved the manuscript. All authors approved the final submission.

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## Declarations

**Conflict of interest** We declare that we have no competing interests.

**Ethical standards** The experiments comply with the current laws of China, where they were performed. Fieldwork was carried out with permission (no. ZL-GZNU-2019-06) from Zhalong National Nature Reserve, Heilongjiang, China. 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-2012-003).

## References

Aidala Z, Croston R, Schwartz J, Tong L, Hauber ME (2015) The role of egg-nest contrast in the rejection of brood parasitic eggs. J Expe Biol 218:1126–1136

Aidala Z, Strausberger BM, Hauber ME (2019) Increased egg-nest visual contrast does not induce egg ejection in the eastern phoebe (*Sayornis phoebe*), an accepter host of the brood parasitic brown-headed cowbird (*Molothrus ater*). J Comp Psych 133:46–55

Antonov A, Stokke BG, Moksnes A, Røskaft E (2007) First evidence of regular common cuckoo, *Cuculus canorus*, parasitism on eastern olivaceous warblers, *Hippolais pallidaelaeica*. Naturwissenschaften 94:307–312

Avilés JM, Soler JJ, Soler M, Møller AP (2004) Rejection of parasitic eggs in relation to egg appearance in magpies. Anim Behav 67:951–958

Avilés JM, Stokke BG, Moksnes A, Røskaft E, Møller ÅM (2006) Rapid increase in cuckoo egg matching in a recently parasitized Reed Warbler population. J Evol Biol 19:1901–1910

Avilés JM, Martín-Gálvez D, De Neve L, Soler M, Soler JJ (2015) Ambient light in domed nests and discrimination of foreign egg colours. Behav Ecol Sociobiol 69:425–435

Bennett ATD, Cuthill IC, Partridge JC, Maier EJ (1996) Ultraviolet vision and mate choice in zebra finches. Nature 380:433–435

Cherry MI, Bennett ATD, Moskát C (2007) Do cuckoos choose nests of great reed warblers on the basis of host egg appearance? J Evol Biol 20:1218–1222

Cuthill IC, Partridge JC, Bennett ATD, Church SC, Hart NS, Hunt S (2000) Ultraviolet vision in birds. Advan in Study Behav 29:159–214

Davies NB (2000) Cuckoos, cowbirds and other cheats. T. & A. D. Poyser, London

Davies NB (2011) Cuckoo adaptations: trickery and tuning. J Zool 284:1–14

Davies NB, Brooke MDL (1989) An experimental study of co-evolution between the cuckoo, *Cuculus canorus*, and its hosts. I. Host egg discrimination. J Anim Ecol 58:207–224

Davies NB, Kilner RM, Noble DG (1998) Nestling cuckoos, *Cuculus canorus*, exploit hosts with begging calls that mimic a brood. Proc Roy Soc B Biol Sci 265:673–678

Feeney WE, Welbergen JA, Langmore NE (2014) Advances in the study of coevolution between avian brood parasites and their hosts. Annu Rev Ecol Evol Sys 45:227–246

Gloag R, Keller LA, Langmore NE (2014) Cryptic cuckoo eggs hide from competing cuckoos. Proc Roy Soc B Biol Sci 281:20141014

Hauber ME, Aidala Z, Igic B, Shawkey MD, Moskát C (2015) Experimental shifts in egg-nest contrasts do not alter egg rejection responses in an avian host-brood parasite system. Anim Cogn 18:1133–1141

Honza M, Šulc M, Jelínek V, Požgayová M, Procházka P (2014) Brood parasites lay eggs matching the appearance of host clutches. Proc Roy Soc B Biol Sci 281:20132665

Honza M, Požgayová M, Procházka P, Koleček J (2020) Errors in egg-laying by female common Cuckoo *Cuculus canorus* in nests of its common host. Ibis 162:637–644

Huo J, Su T, Niu N, Yang C, Liang W (2018) Last but not the least: effects of laying sequence on egg colour variation and embryonic development of russet sparrow (*Passer cinnamomeus*). Avian Res 9:21

Kilner RM (2003) How selfish is a cowbird nestling? Anim Behav 66:569–576

Kilner RM (2006) The evolution of egg colour and patterning in birds. Biolo Rev 81:383–406

Langmore NE, Stevens M, Maurer G, Kilner RM (2009) Are dark cuckoo eggs cryptic in host nests? Anim Behav 78:461–468

Li D, Ruan Y, Wang Y, Chang AK, Wan D, Zhang Z (2016) Egg-spot matching in common cuckoo parasitism of the Oriental reed warbler: effects of host nest availability and egg rejection. Avian Res 7:21

Liang G, Yang C, Wang L, Liang W (2014) Variation in parasitism rates by common cuckoos among three populations of the Oriental reed warblers. Sichuan J Zool 33:673–677

Lyu N, Liang W (2021) Parasitism is always costly to the host. Zool Res 42:217–220

McCormick-Goodhart M, Wilhelm H (2003) A new test method based on CIELAB Colourimetry for evaluating the permanence of pictorial images. Wilhelm Imaging Res. http://www.wilhelm-research.com/articles-wir-additional.html

Medina I, Langmore NE (2019) Nest illumination and the evolution of egg rejection in hosts of brood parasites. Auk 136:1–6

Moksnes A, Røskaft E, Braa AT, Korsnes L, Lampe HM, Pedersen HC (1991) Behavioural responses of potential hosts towards artificial cuckoo eggs and dummies. Behaviour 116:64–89

Moksnes A, Fossø F, Røskaft E, Stokke BG (2013) Reviewing 30 years of studies on the common cuckoo: accumulated knowledge and future perspectives. Chin Birds 4:3–14

Moskát C (2005) Nest defence and egg rejection in great reed warblers over the breeding cycle: are they synchronised with the risk of brood parasitism? Ann Zool Fenn 42:579–586

Peer BD, Sealy SG (2004) Fate of grackle (*Quiscalus* spp.) defenses in the absence of brood parasitism: implications for long-term parasite-host coevolution. Auk 121:1172–1186

Rajchard J (2009) Ultraviolet (UV) light perception by birds: a review. Vet Med 54:351–359

Robertson AR (2007) Colourimetry-Part 4: CIE 1976 $L^*a^*b^*$ colour space. CIE DS014-4.3/E. CIE Central Bureau, Vienna

Røskaft E, Moksnes A, Stokke BG, Bicík V, Moskát C (2002) Aggression to dummy cuckoos by potential European cuckoo hosts. Behaviour 139:613–628

Rothstein SI (1990) A model system for coevolution: avian brood parasitism. Ann Rev Ecol Sys 21:481–508

Ruxton GD, Broom M, Colegrave N (2001) Are unusually coloured eggs a signal to potential conspecific brood parasites? Am Nat 157:451–458

Samaš P, Hauber ME, Cassey P, Grim T (2014) Host responses to interspecific brood parasitism: a by-product of adaptations to conspecific parasitism? Front Zool 11:34

Samaš P, Rutila J, Grim T (2016) The common redstart as a suitable model to study cuckoo-host coevolution in a unique ecological context. BMC Evol Biol 16:255

Samaš P, Rutila J, Honza M, Kysučan M, Grim T (2018) Rearing a virulent common cuckoo is not extra costly for its only cavity-nesting host. Proc Roy Soc B Biol Sci 285:20181710

Samaš P, Grim T, Jelínek V, Abraham MM, Šulc M, Honza M (2019) No immediate or future extra costs of raising a virulent brood parasite chick. Behav Ecol 30:1020–1029

Sealy SG, Underwood TJ (2012) Egg discrimination by hosts and obligate brood parasites: a historical perspective and new synthesis. Chin Birds 3:274–294

Soler M (2014) Long-term coevolution between avian brood parasites and their hosts. Biol Rev 89:688–704

Soler JJ, Soler M, Pérez-Contreras T, Aragón S, Møller AP (1999) Antagonistic antiparasite defenses: nest defence and egg rejection in the magpie host of the great spotted cuckoo. Behav Ecol 10:707–713

Šulc M, Procházka P, Capek M, Honza M (2016) Birds use eggshell UV reflectance when recognizing non-mimetic parasitic eggs. Behav Ecol 27:677–684

Thorogood R, Kilner R, Rasmussen JL (2017) Grey gerygone hosts are not egg rejecters, but shining bronze-cuckoos lay cryptic eggs. Auk 134:340–349

Trnka A, Požgayová M, Procházka P, Prokop P, Honza M (2012) Breeding success of a brood parasite is associated with social mating status of its host. Behav Ecol Sociobiol 66:1187–1194

Wang L, Yang C, Møller AP, Liang W, Lu X (2015) Multiple mechanisms of egg recognition in a cuckoo host. Behav Ecol Sociobiol 69:1761–1767

Wang L, Yang C, He G, Liang W, Møller AP (2020a) Cuckoos use host egg number to choose host nests for parasitism. Proc Roy Soc B Biol Sci 287:20200343

Wang L, Zhong G, He G, Zhang Y, Liang W (2020b) Egg laying behavior of common cuckoos (*Cuculus canorus*): Data based on field video-recordings. Zool Res 41:458–464

Wang L, Zhang Y, Liang W, Møller AP (2021) Common cuckoo females remove more conspicuous eggs during parasitism. Roy Soc Open Sci 8:201264

Xiao F, Yang C, Shi H, Wang J, Sun L, Lin L (2016) Background matching and camouflage efficiency predict population density in four-eyed turtle (*Sacalia quadriocellata*). Behav Proc 131:40–46

Yang C, Liang W, Antonov A, Cai Y, Stokke BG, Fossøy F, Moksnes A, Røskaft E (2012) Diversity of parasitic cuckoos and their hosts in China. Chin Birds 3:9–32

Yang C, Li D, Wang L, Liang G, Zhang Z, Liang W (2014) Geographic variation in parasitism rates of two sympatric cuckoo hosts in China. Zool Res 35:67–71

Yang C, Huang Q, Wang L, Jiang A, Stokke BG, Fossøy F, Møller AP (2016a) Plaintive cuckoos do not select tailorbird hosts that match the phenotypes of their own eggs. Behav Ecol 27:835–841

Yang C, Wang L, Liang W, Møller AP (2016b) Do common cuckoos (*Cuculus canorus*) possess an optimal laying behaviour to match their own egg phenotype to that of their Oriental reed warbler (*Acrocephalus orientalis*) hosts? Biol J Linn Soc 117:422–427

Yang C, Wang L, Liang W, Møller AP (2019) High egg rejection rate in a Chinese population of grey-backed thrush (*Turdus hortulorum*). Zool Res 40:226–230