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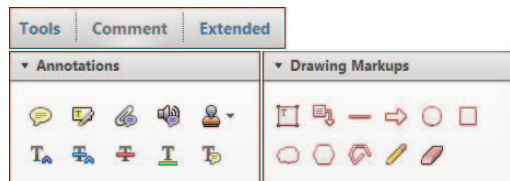
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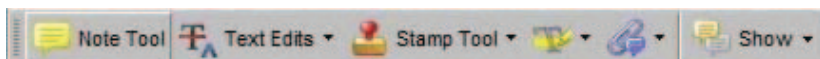
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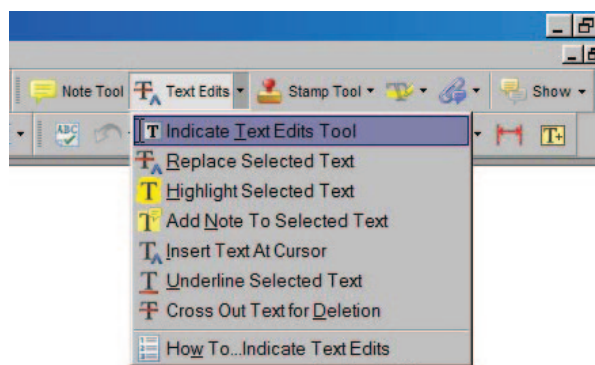
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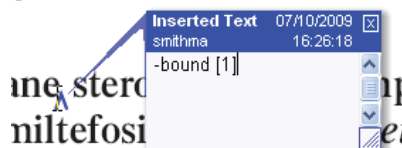
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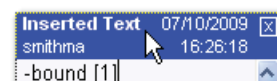
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Original Article

Plaintive cuckoos do not select tailorbird hosts that match the phenotypes of their own eggs

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Received 2 February 2015; revised 30 November 2015; accepted 5 December 2015.

Laying a mimetic egg is important for a brood parasite to succeed in defeating the defenses of a host that can recognize and reject nonmimetic foreign eggs. Several recent studies suggest that common cuckoos (*Cuculus canorus*) do not lay eggs randomly in their regular hosts' nests but select host individuals after inspecting their eggs to maximize the degree of mimicry. The generality of this strategy among brood parasites is, however, not currently known. Here, we studied the matching in egg appearance between plaintive cuckoos (*Cacomantis merulinus*) and their common tailorbird (*Orthotomus sutorius*) hosts, both of which have evolved dimorphic blue and white egg phenotypes with brownish spots, presumably as a result of frequency-dependent selection. Experimental parasitism with eggs of the opposite phenotype to that of the host showed that tailorbirds were very sensitive to the appearance of foreign eggs. Tailorbirds ejected all eggs that differed from the eggs of its own morph while accepting almost all eggs belonging to their corresponding morph. Hence, cuckoos would benefit greatly by selecting host nests with egg phenotypes similar to their own. However, cuckoo eggs only matched the host egg morph in approximately half of the cases, which was consistent with the expected frequency from random egg laying. Therefore, we provide evidence that plaintive cuckoos lay eggs randomly with respect to host egg morph and that they do not selectively choose host nests to maximize egg mimicry and acceptance.

Key words: *Cacomantis merulinus*, egg matching, egg polymorphism, frequency-dependent selection, *Orthotomus sutorius*.

INTRODUCTION

The arms race between obligate parasitic cuckoos and their hosts is regarded as a model system of coevolution, and it has attracted great interest from numerous scientists ever since Aristotle (Davies 2011; Soler 2014). An important stage in this battle occurs during egg laying. Laying a mimetic egg is important for a parasitic cuckoo in order to successfully defeat the defenses of a host that has evolved the ability to recognize and reject nonmimetic foreign eggs. Thus, some species of parasitic cuckoos have been found to diverge into different host races (so-called gentes) that lay a variety of egg morphs (each individual female laying only one egg color type) differing in general appearance but matching their hosts' eggs due to specialization on different host species (Moksnes and Røskoft 1995; Gibbs et al. 2000; Spottiswoode and Stevens 2010; Igic et al.

2012; Langmore and Spottiswoode 2012), although some cuckoos may produce a "general" egg type suited for utilization of several host species (Stoddard and Stevens 2010; Feeney et al. 2014).

The evolution of mimetic eggs in cuckoos may lead to selection on more intricate host defenses, like increased variation in egg appearance among individuals (i.e., increased inter-clutch variation) (Davies and Brooke 1989; Øien 2000; Stokke et al. 2002; Kilner 2006; Yang et al. 2010). Hence, within a particular host species, cuckoo eggs may be mimetic in some nests but nonmimetic in others. The latter ones are prone to be rejected by the host, indicating that cuckoos should select nests in which their egg corresponds to the host eggs' appearance. Some recent studies have found support for this hypothesis (Avilés et al. 2006; Cherry et al. 2007; Honza et al. 2014), whereas others have not (Antonov et al. 2012). Firstly, Avilés et al. (2006) analyzed temporal changes in the degree of matching between common cuckoos (*Cuculus canorus*) and their reed warbler (*Acrocephalus scirpaceus*) hosts and found that some aspect of cuckoo egg reflectance was more similar to that of

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host eggs at parasitized nests than nonparasitized ones, suggesting active host selection by cuckoos. Both Cherry et al. (2007) and Honza et al. (2014) found that the cuckoo eggs were more mimetic to the eggs of their naturally parasitized nests of great reed warblers (*A. arundinaceus*) than to those of their nonparasitized neighbors. However, in a similar approach, Antonov et al. (2012) found no support for cuckoo-egg matching in the marsh warbler (*A. palustris*) and emphasized that cuckoos do not examine host eggs before laying. Anyway, most previous studies suggested that active host selection was based on egg phenotype, and this opinion tends to be accepted by most scientists so far because laying eggs randomly was supposed to be very wasteful thereby violating optimality theory (Parker and Maynard Smith 1990). Furthermore, all previous studies have focused on the common cuckoo and its hosts. Hence, we do not know the generality of active host selection among different species of cuckoos.

Here, we first studied egg rejection rates and egg mimicry in plaintive cuckoos (*Cacomantis merulinus*) and one of their regular hosts, the common tailorbird (*Orthotomus sutorius*). Secondly, we tested if active host selection based on egg phenotype matching is taking place in this host–parasite system.

MATERIALS AND METHODS

Study area and study species

This study was performed in Nonggang (NG) National Nature Reserve, Guangxi Zhuang Autonomous Region, Southwestern China, during the breeding seasons April–July 2011–2014. NG is located in the Sino-Vietnamese border region (22°13'N, 106°42'E), a typical limestone area with an altitude ranging between 150 and 650 m. It is located in the northern margin of the tropics with a mean annual rainfall of 1150–1550 mm and a mean annual temperature of 20.8–22.4 °C (Zhou and Jiang 2008; Jiang et al. 2013). The common tailorbird is one of the most abundant species in NG, and it builds its nest in bushes by stitching leaves together (Figure 1a). In the study area, there are 2 additional tailorbird species breeding in similar habitats: the mountain tailorbird (*O. cuculatus*) and the dark-necked tailorbird (*O. atrogularis*). The plaintive cuckoo is one of the smallest parasitic cuckoo species in Asia, with a body mass of only 21.3–27.2 g ($n = 10$) (Payne 2005), and its chicks are characterized by a rufous plumage with black bars that is similar to that of adult females (Figure 1b). The coevolutionary history between plaintive cuckoos and their hosts is still largely unknown, and so far the only information comes from anecdotal records of parasitism in a few host species (Payne 2005; Erritzøe et al. 2012). We located tailorbird nests by systematically searching potential nest sites and monitoring adult activities. Tailorbird eggs in nests found before or during the laying period were marked with a marker pen and monitored every day to identify parasitism by plaintive cuckoos.

Ethical note

The experiments comply with the current laws of China, where they were performed. Fieldwork was carried out under the permission from Nonggang National Nature Reserve, Guangxi, China. All experimental procedures, including eggs collected in 2014 for color measurement and for another study of nestlings (by O.H.T. from Norwegian University of Science and Technology, Norway), were in agreement with the Animal Research Ethics Committee of Hainan Provincial Education Centre for Ecology and Environment, Hainan Normal University (no. HNECEE-2012-002).

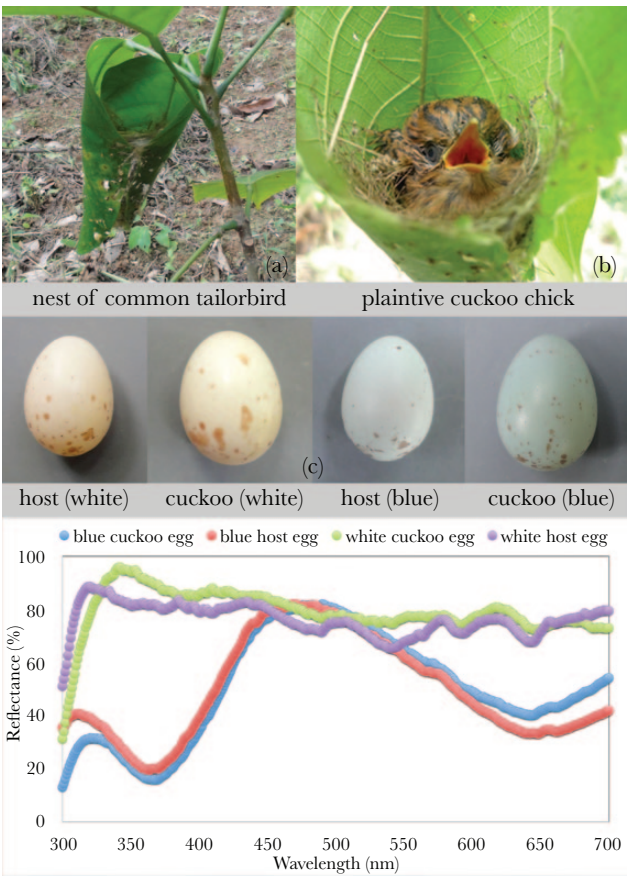


Figure 1
Photos of (a) a common tailorbird nest, (b) a plaintive cuckoo chick, and (c) dimorphic eggs of host and cuckoo, and the reflectance spectra corresponding to the cuckoo and host eggs in the photos.

Experimental parasitism with crossing egg phenotypes

Both the common tailorbirds and plaintive cuckoos were found to lay white or blue egg with brown spots (Figure 1c), and a crossing design of egg phenotypes (Yang et al. 2014a) was used to test for egg discrimination in tailorbirds by adding consistent or contrasting conspecific eggs into their nests. In such an experimental design, nests of either blue or white clutches were randomly sorted into 1) a contrasting group, in which a conspecific egg of contrasting phenotype (i.e., blue to white or white to blue) was introduced into a host nest ($n = 10$ and 13 for blue and white clutches, respectively), 2) a consistent group, in which a conspecific egg of consistent phenotype (i.e., blue to blue or white to white) was introduced into a host nest ($n = 13$ and 15 for blue and white clutches, respectively), or 3) a control group, in which a nest was visited by the same procedure without manipulation to control for human disturbance ($n = 10$ and 11 for blue and white clutches, respectively). Experiments were carried out on the day soon after host clutches were completed and subsequently monitored for 6 days to investigate host responses, which were classified as 1) rejection if foreign eggs were ejected or deserted by hosts, or 2) acceptance if foreign eggs were accepted and incubated together with their own eggs.

Egg matching between cuckoos and hosts

We recorded egg phenotypes of both hosts and cuckoos in all nests found. We checked the ground under nests to investigate the possibility of egg rejection by hosts before our visits. Egg length and width were measured with a vernier caliper and egg volumes were calculated by using the formula developed by Hoyt (1979) ($n = 24$ for both cuckoos and hosts). One egg from each nest was randomly selected for egg size comparison.

Egg color (ground and marking) and egg pattern of tailorbirds and cuckoos ($n = 24$ for both species) were analyzed with Vorobyev–Osorio models controlling for avian vision and granularity analysis, respectively (Stoddard and Stevens 2010). For egg color of ground and markings, reflectance spectra were measured with a spectrometer (Avantes-2048, Avantes, Apeldoorn, The Netherlands). We used average spectral sensitivity curves for UVS-type avian retinas provided by Endler and Mielke (2005). Chromatic and achromatic contrasts between cuckoo and host eggs were calculated by just noticeable differences (JND) in Vorobyev–Osorio models for egg color, whereas egg pattern sizes of marking were quantified by granularity analysis from small to large with 7 spatial scales, represented by 7 filter sizes (1, 2, 4, 8, 16, 32, and 64). The larger and smaller filter sizes refer to smaller and larger egg markings, respectively. JND is the unit for perceptual difference between 2 spectra, and it increases as the discrimination of 2 colors is predicted to increase. For further details of these analyses, see Vorobyev et al. (1998), Vorobyev and Osorio (1998), Stoddard and Stevens (2010), and Yang et al. (2014b). All egg spectra were obtained in 2014 except for those of 2 clutches (1 blue host clutch with a blue cuckoo egg and 1 white clutch with a blue cuckoo egg) obtained in 2013. For the egg spectra from 2014, the matched clutches ($n = 9$) consisted of 8 cases of natural parasitism (6 white host clutches with white cuckoo eggs and 2 blue host clutches with blue cuckoo eggs) and 1 case of a cuckoo nest choice experiment (blue clutch with blue cuckoo egg; see below), whereas the unmatched clutches ($n = 13$) consisted of 11 cases of natural parasitism (4 white clutches with blue cuckoo eggs and 7 blue clutches with white cuckoo eggs) and 2 cases of cuckoo nest choice experiments (1 white clutch with blue cuckoo eggs and 1 blue clutch with white cuckoo egg). In summary, the sample sizes for spectra measurements in matched and unmatched clutches were 10 and 14, respectively. Additionally, all collected cuckoo eggs were intact when they were detected in the field. All cuckoo eggs were found during the laying period of the host, and the 2 cases of cuckoo eggs for spectra in 2013 were returned to the host nests after measurement, whereas in 2014 all cuckoo eggs found were collected for spectra measurement and for nestling experiments for another study (for more details, see Supplementary Table 1).

Cuckoo nest choice experiment

Because nest selection by cuckoos can be restricted by the number of active nests having the correct phenotype, we performed a cuckoo nest choice experiment where we placed host nests having different egg morphs close together. This ensured that the cuckoo had a real choice of matched and unmatched host eggs in close proximity of each other. In this experiment, 2 nests, each containing 2 immaculate model eggs (2 blue model eggs in one nest and 2 white model eggs in the other, $n = 14$ for both groups), were translocated close to an active but empty host nest (i.e., nest building was just completed, $n = 14$) with a distance of 1.5 m between each pair of nests (i.e., the position of 3 nests was located in the angles

of a triangle), and the nests were then monitored for 6 days twice per day (once in the morning and once in the afternoon). The nests used for experiments were natural nests that had been deserted or depredated during egg laying or in early incubation. The whole branch (ca. 1.5 m) with the nest attached was translocated. A plastic bag with soil and water was bound to the cut surface of each branch to keep it fresh during the experiment.

Statistical analyses

Statistical analyses were performed in IBM SPSS 20.0 (IBM Inc.). Either Student's t -test (if variances were equal) or Welch's t -test (if variances were not equal) was used to compare JND between matched and unmatched parasitized nests, whereas a paired-sample t -test was used to compare the normalized energies (i.e., refers to relative contribution of different marking sizes to the overall egg markings) between cuckoo and host eggs among different filter sizes. Fisher's exact test was used for the comparison of proportions of data, whereas goodness-of-fit test was used for testing an observed frequency against a theoretical expectation. Values are presented as mean \pm standard deviation and significance level was set to $P < 0.05$. Visual modeling was established in Matlab 2012a (MathWork Inc.).

RESULTS

Egg discrimination by tailorbirds

No nest desertion or egg ejection was found in the control group within 24 h after the manipulation for either blue ($n = 10$) or white ($n = 11$) clutches. Tailorbird hosts with blue clutches ejected 100% of conspecific white eggs ($n = 10$) but accepted 100% of conspecific blue eggs ($n = 13$; Table 1). Similarly, tailorbird hosts with white clutches ejected 100% of conspecific blue eggs ($n = 13$) and accepted nearly all conspecific white eggs (93.3%, $n = 15$). Thus, they ejected at similar rates whether the host laid blue or white eggs (Fisher's exact test; $P = 1.000$) and accepted at similar rates for similar conspecific egg phenotypes (Fisher's exact test; $P = 1.000$). All rejection occurred within the first day after the parasitism experiment, whereas no rejection errors (i.e., disappearance of own eggs together with the parasitic egg) were detected in all ejections. Rejected eggs disappeared without leaving any visible signs (e.g., remains of shell or egg content inside or under the nest), possibly because hosts ejected them and carried them far away from the nests.

Cuckoo parasitism and egg matching

The common tailorbird has a clutch size of $4.2 \text{ eggs} \pm 0.7$ ($n = 171$). The general parasitism rate in common tailorbirds was 17.0% (41 out of 241 nests), with annual variation from 2011 to 2014 (i.e., 2011: 16.0%, $n = 25$; 2012: 8.3%, $n = 24$; 2013: 15.1%, $n = 86$; 2014: 20.8%, $n = 106$) that was not significantly different (chi-square test; $\chi^2 = 2.569$, degrees of freedom [df] = 3, $P = 0.463$). Common tailorbirds laid blue ($n = 122$) or white ($n = 119$) eggs, both with brown spots (Figure 1c). Individual hosts consistently laid either white or blue eggs; the 2 types were never found in the same nest. The proportion of blue and white egg phenotypes in this study population was not statistically different from the ratio of 1:1 (ratio of blue and white eggs in the population were 50.6% and 49.4%, respectively) (goodness-of-fit test; $\chi^2 = 0.019$, df = 1, $P = 0.891$), and the size of white and blue eggs was not statistically different ($1.06 \pm 0.10 \text{ cm}^3$ [$n = 12$]; $1.06 \pm 0.07 \text{ cm}^3$ [$n = 12$]; Student's t -test; $t = 0.124$, df = 22, $P = 0.902$).

Plaintive cuckoos also laid blue ($n = 16$) and white eggs ($n = 25$), and the ratio was not statically different from the ratio of 1:1 (goodness-of-fit test; $\chi^2 = 1.012$, $df = 1$, $P = 0.379$) or from the ratio of blue and white eggs laid by the hosts (Fisher's exact test; $P = 0.181$). However, cuckoo eggs were laid in host nests having eggs matching their own phenotype in only 48.8% of the cases (Table 1), which was not statistically different from random (i.e., the random distribution of cuckoo eggs among available host nests; goodness-of-fit test; $\chi^2 < 0.001$, $df = 1$, $P = 1$). We have not found mismatching eggs that were rejected on the ground under the nests of the hosts. The mean size of cuckoo eggs was $1.51\text{ cm}^3 \pm 0.12$ ($n = 24$), which was significantly larger than the host eggs (Student's t -test; $t = 14.89$, $df = 46$, $P < 0.001$). All cuckoo eggs were laid during the egg-laying period of their tailorbird hosts. However, we found that

tailorbirds did not incubate their eggs and reject cuckoo eggs during the egg-laying period. All rejection of unmatched cuckoo eggs was performed by ejection ($n = 10$) and occurred on the first day after the initiation of incubation. This result is consistent with the result of the parasitism experiment, which was performed on the first day after completion of host clutches. Furthermore, all rejected eggs were found to disappear from host nests. In 2014, the responses to the cuckoo eggs found by hosts were not investigated because we collected all eggs for spectra measurement and for nestling experiments for another study (for more details, see Supplementary Table 1). Additionally, all cuckoo eggs that were detected by the observer before rejection by hosts were intact in host nests. We did not find any case of cuckoo eggs that were rejected onto the ground under the host nests.

Table 1
Egg-laying matching in common tailorbirds by plaintive cuckoos, with parasitism rates in parentheses

Host clutch	Number of nests	Number of parasitized nests (% parasitism)	Observed frequency		Expected frequency ^a		χ^2	df	P^b
			Matched	Unmatched	Matched	Unmatched			
Blue	122	19 (15.6)	7	12	8.1	12.7	<0.001	1	1
White	119	22 (18.5)	13	9	12.3	7.9			
Total	241	41 (17.0)	20	21	20.4	20.6			

^aThe expected frequency refers to a random distribution of 25 white and 16 blue cuckoo eggs among the available 241 host nests.
^bChi-square test for comparison between total observed and expected frequencies.

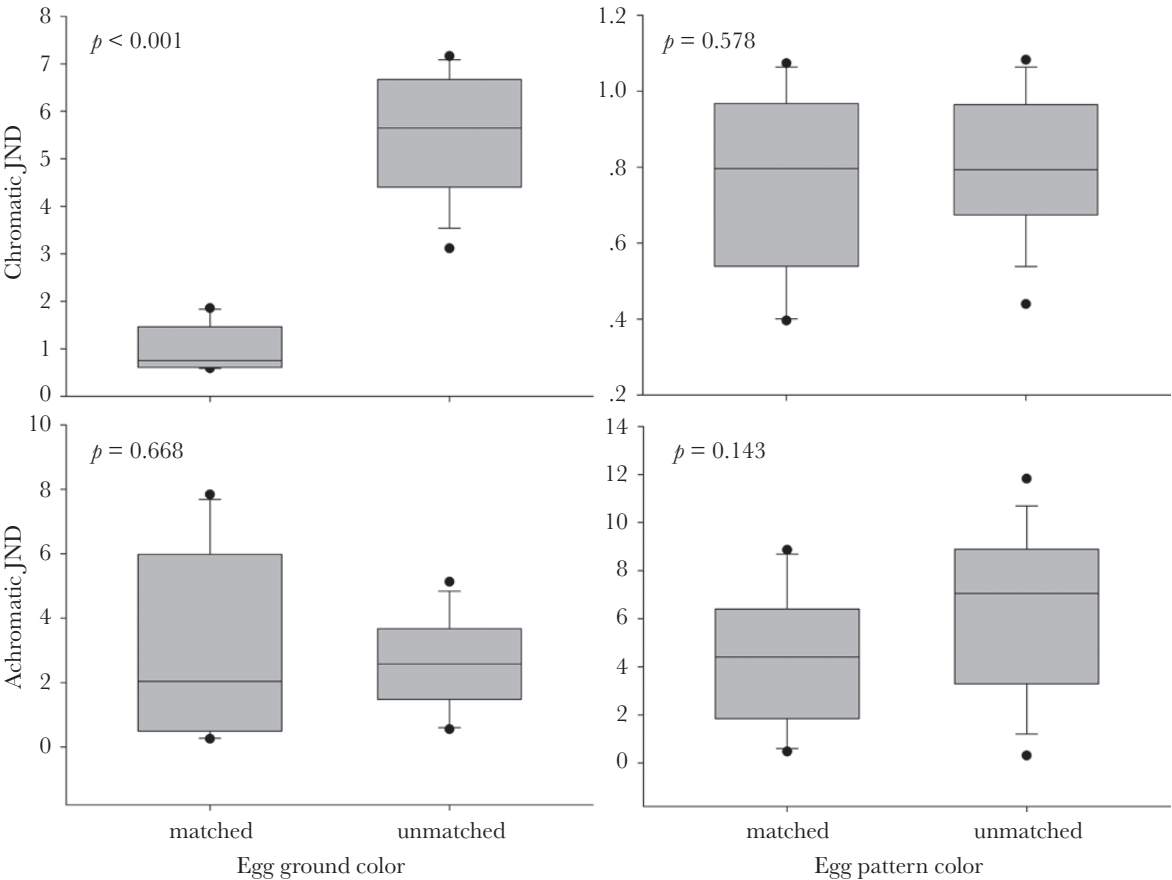


Figure 2
 Comparison of JND between matched ($n = 10$) and unmatched ($n = 14$) parasitized nests of the common tailorbird (12 clutches for blue and white color, respectively). Boxplots indicate median, 10th, 25th, 75th, and 90th percentiles with whiskers as error bars and dots as outliers. P values reflect differences between eggs with matching and unmatching ground color and eggs with matching and unmatching egg color pattern.

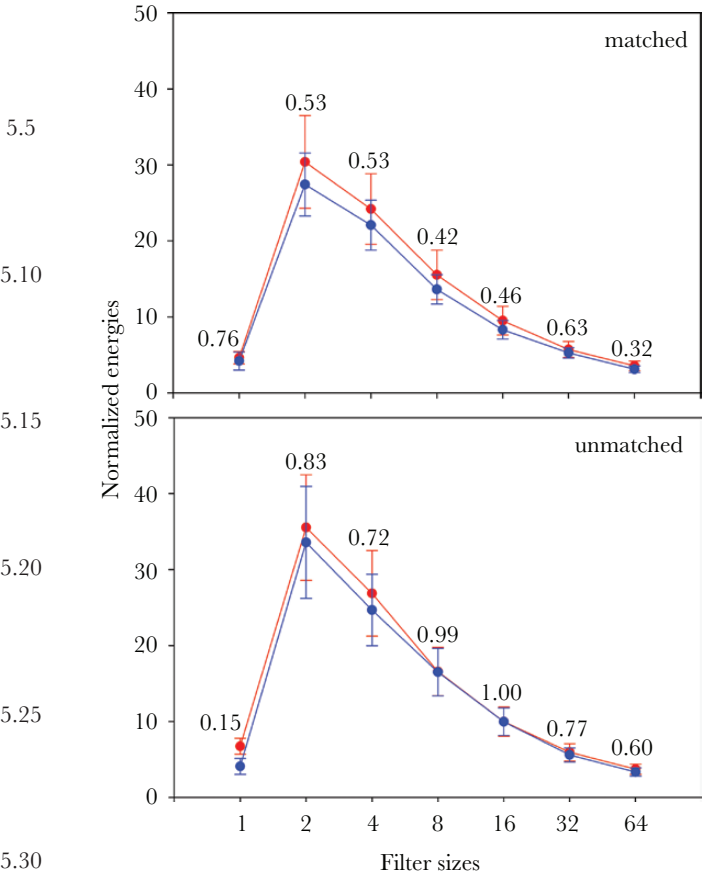


Figure 3
 Granularity analysis of egg pattern mimicry in matched ($n = 10$) and unmatched ($n = 14$) parasitized nests of the common tailorbird. Normalized energies refer to relative contribution of different marking sizes to the overall egg markings between cuckoo and host eggs among different filter sizes. Red and blue circles refer to cuckoo and host, respectively. Numbers on lines refer to the P values from paired-sample t -test. Error bars = standard error.

Table 2
Response to experimental parasitism using different conspecific egg morphs of common tailorbird

		Accepted	Ejected	Deserted	Total nests	Rejection rate (%)
5.45	Blue clutch					
	Conspecific blue egg	10	0	0	10	0
	Conspecific white egg	0	13	0	13	100
5.50	White clutch					
	Conspecific white egg	14	1	0	15	6.67
	Conspecific blue egg	0	13	0	13	100

Visual modeling illustrated that the JND of the chromatic component between cuckoo and host eggs in unmatched nests was significantly larger than in matched nests (Welch's t -test; $t = -11.89$, $df = 17.7$, $P < 0.001$, Figure 2). This is consistent with the detection of differences between blue and white egg phenotypes by human vision because chromatic JND refers to the color hue. However, JND of the achromatic component, which refers to luminance, did

Table 3
Results from the cuckoo nest choice experiment

Active nests with blue or white tailorbird eggs	Artificial nests with immaculate blue and white model eggs near the active nests	
Blue clutch (blue cuckoo egg)	Blue clutch	White clutch
Blue clutch (white cuckoo egg)	Blue clutch	White clutch
White clutch (blue cuckoo egg)	Blue clutch	White clutch (blue cuckoo egg)
White clutch	Blue clutch	White clutch (white cuckoo egg)

Eggs laid by cuckoos are indicated in parentheses.

not differ significantly between matched ($n = 10$) and unmatched ($n = 14$) parasitized nests (Welch's t -test; $t = 0.439$, $df = 12.3$, $P = 0.67$). Likewise, differences in spot color did not reach statistical significance for either chromatic or achromatic JND (Student's t -tests; chromatic: $t = -0.565$, $df = 22$, $P = 0.578$; achromatic: $t = -1.52$, $df = 22$, $P = 0.143$). Furthermore, a granularity analysis showed that the egg pattern did not differ between cuckoo and host eggs for either matched or unmatched parasitized nests for any of the filter sizes (Figure 3).

Cuckoo nest choice experiment

In total, 14 pairs of translocated nests (i.e., 28 nests) were mounted near 14 active tailorbird host nests (6 white clutches and 8 blue clutches) to investigate selective egg laying by cuckoos. However, among the 14 trios of nests, only 3 active nests and 2 translocated nests were utilized by cuckoos (Table 3). For the 3 active nests, 1 blue tailorbird clutch was matched by 1 blue cuckoo egg, whereas 2 unmatched cuckoo eggs were laid in 2 other clutches (1 blue cuckoo egg in a white clutch and 1 white cuckoo egg in a blue tailorbird clutch). The 2 parasitized translocated nests both contained white model eggs and were parasitized by 1 blue and 1 white cuckoo egg. All 5 cuckoo eggs were laid on the second day of egg laying (i.e., on the day hosts laid their second egg).

DISCUSSION

Host use, egg rejection, and egg mimicry

To our knowledge, 15 species have so far been recorded as hosts of plaintive cuckoos, including 5 species of tailorbird (*Orthotomus* spp.), 5 species of prinia (*Prinia* spp.), 2 species of iora (*Aegithina* spp.), 1 species of spiderhunter (*Arachnothera* sp.), 1 species of cisticola (*Cisticola* sp.), and 1 species of sunbird (*Aethopyga* sp.) (Payne 2005; Erritzøe et al. 2012; Yang et al. 2012). According to previous descriptions of cuckoo egg morphs from nests of 5 different host species (Payne 2005), cuckoo eggs were white or blue in background color with markings, which is similar to our observations in this study. In our study area, plaintive cuckoos mainly utilize common tailorbirds, whereas mountain tailorbirds, which also lay polymorphic eggs (blue or white with or without markings), are only occasionally parasitized. However, the interactions between this brood parasite and its hosts are still poorly understood (Payne 2005; Erritzøe et al. 2012). Here, we have documented coevolutionary interactions between the plaintive cuckoo gentes parasitizing common tailorbirds. Avian visual modeling confirmed that tailorbirds lay dimorphic blue or white eggs, which were

significantly different in ground color but not in marking color or pattern. Plaintive cuckoos appeared to have evolved corresponding dimorphic eggs, and such polymorphic egg phenotypes are most likely an adaptation to brood parasitism (Lahti 2005; Spottiswoode and Stevens 2010; Yang et al. 2010; Vikan et al. 2011). Moreover, tailorbirds were very sensitive to the appearance of foreign eggs because they ejected all conspecific phenotypes differing from their own morph. This indicates that tailorbirds have experienced strong selection from brood parasites resulting in the evolution of dimorphic eggs, whereas plaintive cuckoos have faced intense selection from tailorbirds that recognize and reject eggs with unmatched phenotypes. Thus, they have evolved correspondingly dimorphic eggs that are highly mimetic in ground color and spotting pattern, but not in egg size. Interestingly, the frequencies of the 2 morphs were almost identical in both hosts and cuckoos, suggesting that frequency-dependent selection generated by the coevolutionary arms race affects the ratios.

Host selection by plaintive cuckoos

Recent studies have found that common cuckoos appear to know their own egg appearance and choose host nests containing matching eggs (Avilés et al. 2006; Cherry et al. 2007; Honza et al. 2014; but see Antonov et al. 2012). Due to the high rejection rate of non-mimetic eggs in tailorbirds, active host selection based on egg phenotype matching should also be advantageous in plaintive cuckoos. However, our investigations failed to find support for this strategy. Although tailorbirds distinguish between different egg phenotypes and reject unmatched eggs, cuckoos laid matched and unmatched egg phenotypes in host nests with an almost identical probability. This result therefore supports random egg laying with respect to host egg color by the plaintive cuckoo. Furthermore, we carefully monitored the fate of cuckoo eggs in host nests in 2011–2013 and found that unmatched cuckoo eggs were all ejected by hosts ($n = 10$) (cuckoo eggs in 2014 were collected for nestling experiments for another study; for more details, see Supplementary Table 1). This finding is consistent with the results from our study on experimental parasitism. Although the parasitism rates we reported here may suffer from a potential bias due to rejection by hosts before we detected cuckoo eggs, we minimized this possibility by daily monitoring of host nests. Furthermore, considering that tailorbirds reject nonmimetic eggs at a considerably higher frequency than mimetic eggs, the parasitism rates in unmatched nests should suffer more from underestimation than in matched nests. Finally, the host nest choice experiment, giving the cuckoo a choice of nests having both matching and nonmatching eggs in close proximity, was consistent with the random egg-laying pattern of plaintive cuckoos, although the sample size was small.

A theoretical model showed that for hosts (*Paradoxornis alphonisianus*) that lay polymorphic eggs, if cuckoos lay eggs by strictly matching those of their hosts, it would considerably limit host shifts, which would reduce expansion of host use in cuckoos (Yang et al. 2015a). Furthermore, a recent study of cuckoo-egg matching between parasitized and nonparasitized nests in a common cuckoo host, the Oriental reed warbler (*A. orientalis*), showed that cuckoo-egg matching in parasitized nests was no better than that in nonparasitized nests (Yang et al. 2015b). Although random egg laying seems to be wasteful for parasitic cuckoos according to optimality theory (Parker and Maynard Smith 1990), the cost and benefit of different egg-laying strategies have not been evaluated. More importantly, unlike egg polymorphism and mimicry for which evolution requires only mutation in pigmentation genes, the matching

laying behavior may not easily evolve because it requires complex behavioral adaptation, and it needs as precondition that cuckoos know their own egg appearance. However, this precondition is just a speculation that has not been proved (Yang et al. 2015b).

In conclusion, tailorbird hosts lay eggs with 2 distinct ground colors, and plaintive cuckoos produce eggs that mimic both of these egg types. Selection on cuckoos for choosing hosts with the corresponding egg type is strong because all nonmimetic eggs were ejected by the host. However, we found no indication of such active host choice by cuckoos in our study population. Our findings provide novel insights into a poorly known cuckoo–host system and highlight the importance of studying such systems to further expand our knowledge of brood parasitism in general.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at <http://www.behco.oxfordjournals.org/>

FUNDING

This work was supported by the National Natural Science Foundation of China (81260514 to C.Y., 31272328 and 31472013 to W.L., 31460567 to A.J.) and Program for New Century Excellent Talents in University (NCET-13-0761 to C.Y.). B.G.S. and F.F. were funded by the Research Council of Norway (218144).

We would like to thank Prof. L. Simmons, Dr W. Forstmeier, and 2 anonymous reviewers for their constructive and helpful comments that greatly improved this manuscript. We are grateful to I. Will, University of California, Berkeley, CA, M. Jiang, and Y. Hu for their assistance with fieldwork. We thank J. Nong and his family for help with logistics.

Conflict of Interest Statement: We declare that all authors have no conflict of interest.

Handling editor: Wolfgang Forstmeier

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