Chinese Birds 2013, 4(1):51–56
DOI 10.5122/cbirds.2013.0004

ORIGINAL ARTICLE

Eggs mimicry of Common Cuckoo (*Cuculus canorus*) utilizing Ashy-throated Parrotbill (*Paradoxornis alphonsianus*) host

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Abstract Polymorphism in egg coloration is prominent in the Common Cuckoo (*Cuculus canorus*) and a common host, the Ashy-throated Parrotbill (*Paradoxornis alphonsianus*). Egg polymorphism has probably evolved as a consequence of frequency-dependent selection in both host and parasite, and has, according to human vision, resulted in discrete immaculate white, pale blue and blue egg phenotypes within a single population. However, egg mimicry assessment is not always straightforward, and previous studies have shown that human based comparisons applied to the coloration of bird eggs may be inadequate. Here, we objectively quantify egg color of both parasite and host by spectrophotometry and assess egg mimicry of the Common Cuckoo to the eggs of its Ashy-throated Parrotbill host. Our results revealed that egg reflectance spectra agree well with the assessment based on human vision that cuckoo eggs mimic those of the parrotbill host, in both visible (VIS) and ultraviolet (UV) ranges. However, the white cuckoo egg shows slightly poorer mimicry than the blue cuckoo egg in corresponding host clutches. We suggest that the white parrotbill egg morph (and subsequently the whitish cuckoo egg color) may have evolved after the evolution of the blue egg morph due to strong selection from parasites in the cuckoo-parrotbill system.

Keywords brood parasitism, egg coloration, egg reflectance, evolutionary lag

Introduction

Trait polymorphism in natural populations can evolve as a consequence of frequency-dependent selection (Majerus, 1998). This implies that parasites, predators or other selective agents impose variable intensities of selection on the phenotype depending on the frequency in the population. Brood parasites and their hosts provide one such possible case of frequency-dependent selection resulting in the evolution of polymorphic eggs in both host and parasite (Kilner, 2006; Yang et al., 2010a). Obligate avian brood parasites lay their eggs in nests belonging to other species of birds, thereby transferring the costs of parental care to their victims. As a consequence, hosts evolve defenses to counter brood parasitism, which in turn selects for corresponding counter-adaptations for better trickery of parasites (Davies and Brooke, 1989). The well-known arms race between parasitic cuckoos and their hosts are regarded as a textbook example of co-evolutionary interactions. Theoretically, the cuckoo-host system, when acting in a frequency-dependent manner, should be able to produce polymorphisms in co-evolved traits in the interacting parties. This hypothetical scenario has been found in the Common Cuckoo (*Cuculus canorus*) and one of its hosts, the Ashy-throated Parrotbill (*Paradoxornis alphonsianus*), in which both species have evolved matching egg polymorphism manifested in discrete immaculate white, pale blue and blue egg phenotypes within a single population (Fig. 1; Yang et al., 2010a). However, egg mimicry assessment is not always

Received 19 December 2012; accepted 20 March 2013

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Fig. 1 Egg polymorphism of Common Cuckoo (*Cuculus canorus*) and Ashy-throated Parrotbill (*Paradoxornis alphonsianus*). (**a**), (**b**) and (**c**) refer to blue, pale blue and white clutches of parrotbill, respectively, with a cuckoo egg (larger egg) being present in each clutch (Photos by C. Yang).

straightforward. Inspection using spectrophotometric methods suggested that the eggs of the Great Spotted Cuckoo (*Clamator glandarius*) were not significantly related to the appearance of its Magpie (*Pica pica*) host eggs (Soler et al., 2003). In the Red-chested Cuckoo (*Cuculus solitarius*), cuckoo eggs actually match the eggs of their hosts most closely at wavelengths that cannot be perceived by the human eye (Cherry and Bennett, 2001). Starling et al. (2006) revealed by reflectance spectrophotometry that the color of Pallid Cuckoo (*Cuculus pallidus*) eggs differed between four host species of Melaphagid Honeyeaters (*Lichenostomus penicillatus, L. chrysops, L. melanops*, and *Melithreptus affinis*), and mimicked their hosts' eggs closely in both spectral shape and brightness. The Pallid Cuckoo eggs from the four different hosts' nests matched their respective hosts closely. However, host eggs exhibited a small peak in the ultraviolet that was not mimicked by the cuckoo eggs (Starling et al., 2006). Using digital image analysis and modelling of avian vision, Stoddard and Stevens (2010) recently showed that various features of host egg pattern are mimicked by the eggs of their respective cuckoo host-race. These studies revealed that cuckoos have host-specific egg types that have not been detected by human observation, and emphasize potential inadequacy of human comparisons applied to the coloration of bird eggs, and the importance of techniques such as spectrophotometry to measure color objectively (Starling et al., 2006).

The objective of this study was to quantify egg color by spectrophotometry and assess the extent of egg mimicry of Common Cuckoo to the eggs of its Ashy-throated Parrotbill host for blue, pale blue and white clutches, respectively.

Methods

Study area

The study was performed in the Kuankuoshui Nature Reserve, Guizhou, south-western China (28°10′N, 107° 10′E) during April–July 2008–2009. The study site is situated in a subtropical moist broadleaf and mixed forest, interspersed with abandoned tea plantations, shrubby areas, and open fields used as cattle pastures (see also Yang et al., 2010a, b).

Egg coloration quantification

Nests were found by systematically searching all typical and potential nest sites and by monitoring the activities of adult hosts throughout the breeding season. We recorded date of the first egg laid, egg color morph, clutch size and occurrence of brood parasitism for each nest. When a nest was found during the incubation period, eggs were floated in water to estimate approximate laying date (Hays and Lecroy, 1971). We used three spectrophotometers for quantification of egg coloration: the USB4000-VIS-NIR, GZ03P and Avantes-2048 to measure the visible (VIS) range (400–700 nm) of blue and white clutches, ultraviolet (UV) range (300–400 nm) of blue and white clutches (Fig. 2) and VIS-UV range (300–700 nm) of pale blue clutches (Fig. 3), respectively (Yang et al., 2009, 2011). Due to equipment limit, we did in such way, which was surely a suboptimal way of doing it. In earlier years, our spectrophotometer can only measure the spectrum range from 400 to 700 nm (VIS). And an additional UV spectrophotometer was used to supplement the UV data. But these data are

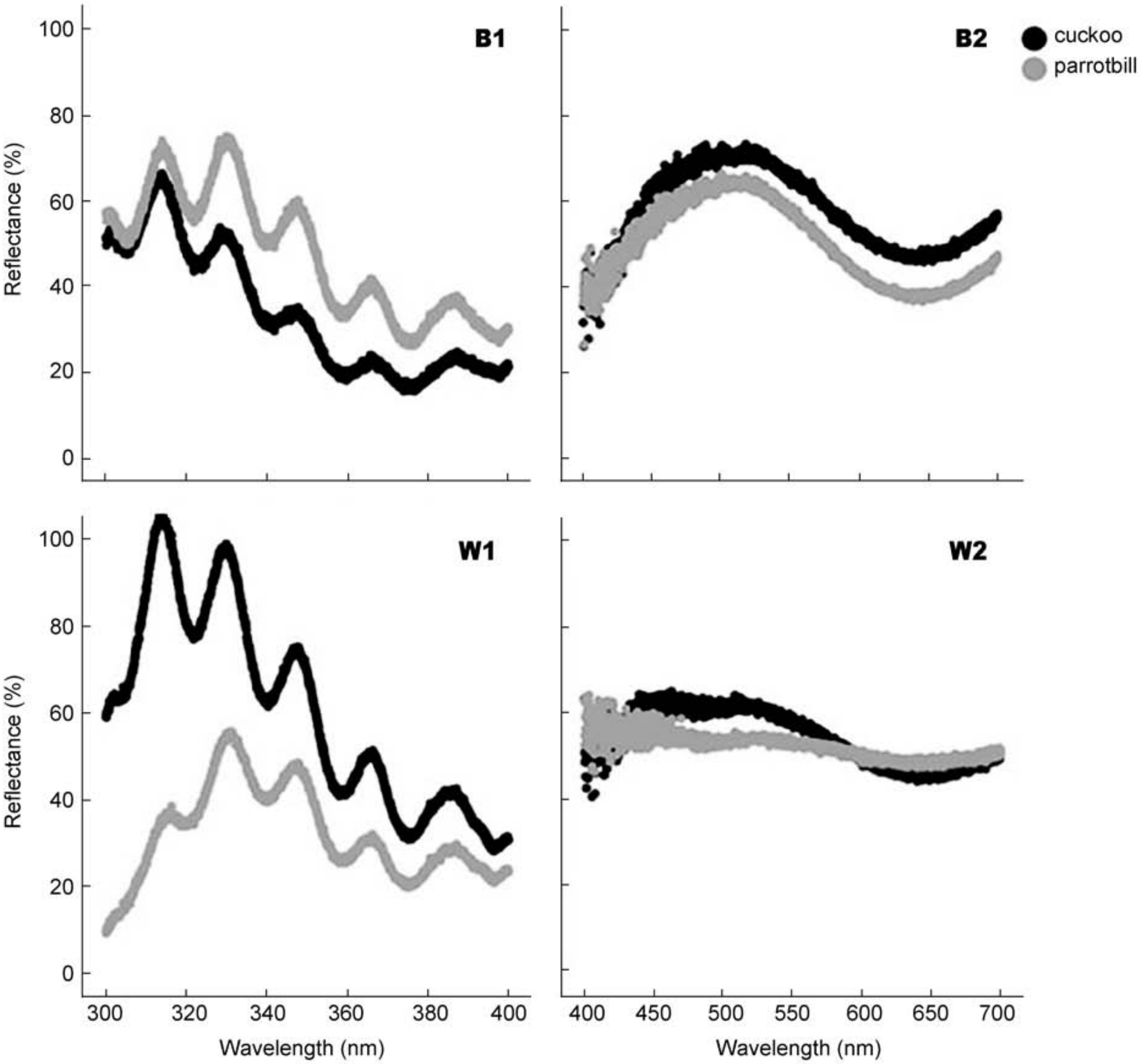

Fig. 2 Ultraviolet and visible reflectance spectrum of the egg phenotypes in Common Cuckoo (*Cuculus canorus*) and Ashy-throated Parrotbill (*Paradoxornis alphonsianus*). The curves represent the spectrum for one cuckoo egg and average spectra for all host eggs in the observed parasitized nest. B1 and B2 refer to the UV and VIS spectrum of blue clutches; W1 and W2 refer to the UV and VIS spectrum of white clutches.

from quite different machines and cannot be merged together. Finally, the pale blue eggs were measured by the Avantes spectrophotometer which covers the spectrum range from 300–700 nm. However, cuckoo eggs were few and phenotypes we found were very variable in different years.

Both the Ashy-throated Parrotbill (hereafter parrotbill) and the Common Cuckoo (hereafter cuckoo) laid immaculate eggs (Fig. 1), and we obtained six measurements of spectral reflectance for each egg, with two at the blunt end, two at the middle and two at the sharp end of the egg. To represent the egg coloration of the cuckoo, the mean of each egg was summarized from these six measurements. For the parrotbill, egg coloration was represented as the mean of all host eggs in each clutch. Each measurement covered ca. 1 mm^2 and was taken at a 45° angle to the egg surface, with the spectrometer and light source connected with a coaxial reflectance probe (Yang et al., 2009, 2010b). We also classified the degree of cuckoo eggs mimicry on a 5-degree scale based on human vision relying on 30 volunteers who scored the degree of mimicry (contrast) from 1 (non-mimetic) to 5 (perfect mimicry) following the approach first developed by Moksnes and Røskaft

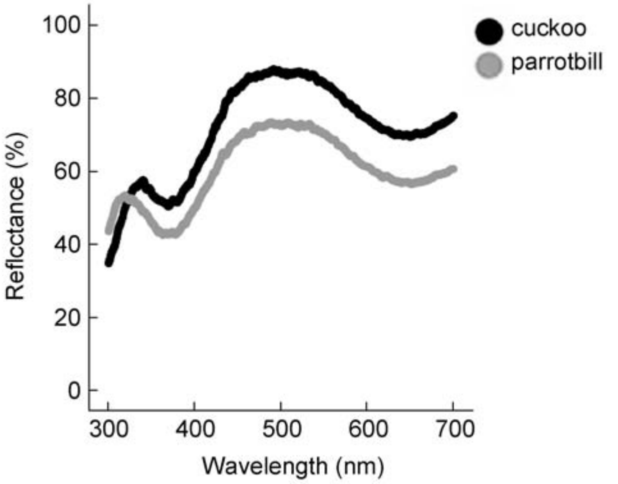

Fig. 3 Ultraviolet and visible reflectance spectra of the pale blue egg phenotype in Common Cuckoo (*Cuculus canorus*) and Ashy-throated Parrotbill (*Paradoxornis alphonsianus*). The curves represent the spectrum for one cuckoo egg and average spectra for all host eggs in the observed parasitized nest.

(1995).

The experiments comply with the current laws of China in which 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.

Data analyses were performed in SPSS 13.0 for Windows (SPSS Inc, Chicago, Illinois). One-way ANOVA and Kruskal-Wallis ANOVA were used for comparison of normally and non-normally distributed data, respectively. Values were presented as mean ± SD.

Results

Mimicry score based on human vision showed that the contrasts between cuckoo and parrotbill eggs of the matched-phenotype (blue versus blue, pale blue versus pale blue, and white versus white) differed significantly among the three egg phenotypes ($\chi^2 = 4.41$, df = 2, $p = 0.015$). The mimicry of blue cuckoo eggs to blue host eggs was the highest and significantly higher than that of the white matched pair (blue: 1.03 ± 0.18 vs. white: 1.30 ± 0.47, $n = 30$ for each category, $p = 0.015$, post hoc test). The mimicry of pale blue cuckoo egg was intermediate between the blue and the white egg (1.13 ± 0.35, $n = 30$), with no statistical significant difference from blue ($p = 0.273$) or white eggs ($p = 0.070$).

Egg reflectance spectra revealed that the wave shape, wave peak and wave trough of cuckoo and parrotbill egg spectrum for the blue phenotype were perfectly matching in both visible (VIS) and ultraviolet (UV) ranges (Figs. 1–2), which indicated that they were very similar in egg color hue and chroma. However, the wave shape of the white cuckoo egg was more variable, with a wave peak in the blue region (Fig. 2), which were lacking in the parrotbill egg. The reflectance spectra for UV between white cuckoo and parrotbill eggs were discrete in 300–340 nm. A similar pattern was found for pale blue cuckoo and parrotbill eggs for which the reflectance curves matched well in wavelengths 340–700 nm.

Discussion

Our results show that egg reflectance spectra agree well with the assessment based on human vision that cuckoo eggs mimic those of the parrotbill host. Our previous studies have also indicated that the classification of parrotbill egg morphs based on human vision is consistent with avian visual modelling (Yang et al., 2010a). The sensitivities of UVS-receptor of many birds are concentrated around 340–400 nm with a peak at 370 nm (Chen et al., 1984; Bennett et al., 1994). Recent work by Aidala et al. (2012) also showed that both the Shining Cuckoo (*Chalcites* [*Chrysococcyx*] *lucidus*) and the Long-tailed Cuckoo (*Urodynamis* [*Eudynamis*] *taitensis*) in New Zealand are predicted to possess the short wavelength-sensitive type 1 (SWS1) opsins with maximal sensitivity in the human-visible violet portion of the short-wavelength light spectrum, and not in the UV. Therefore, the UV curves for the three egg phenotypes in cuckoo and its parrotbill host should be regarded as well matching.

The likelihood of nest predation was not significantly different between nests with white and blue egg in the parrotbill (Yang et al., 2010a). Furthermore, other *Paradoxornis* species that have no known history of interaction with the cuckoo lay monomorphic eggs in blue color (Jiang et al., 2009; Yang et al., 2011). Given that the cuckoo ancestrally had egg colors that were neither white nor blue (Davies, 2000), it was reasonable to conclude that nest predation is not responsible for the evolution of egg polymorphism in the parrotbill, and selection on the cuckoo for countering the evolution of multiple parrotbill egg types was evidenced by hosts generally having evolved good abilities to reject even partly mimetic eggs (Yang et al., 2010a).

However, we found that mimicry of blue cuckoo eggs is better than that of white cuckoo eggs in their corresponding host clutches, implying that the white morph may potentially be a secondary egg morph that has not yet evolved fine mimetic features.

In conclusion, we have shown evidence from photospectrometry that different egg color morphs in the Cuckoo have evolved in response to selection against poor mimics imposed by parrotbill hosts. This evidence supports the hypothesis that the white egg morph in the cuckoo-parrotbill system might be a secondary phenotype that has evolved under the strong selection pressure of brood parasitism.

Acknowledgements We are grateful to Anders P. Møller for valuable comments that significantly improved the quality of the manuscript. We thank Eivin Røskaft, Bård G. Stokke and one anonymous reviewer for helpful comments on our manuscript. This work was supported by the National Natural Science Foundation of China (Nos. 31071938 and 31272328 to WL, 31101646 and 31260514 to CY), Program for New Century Excellent Talents in University (NCET-10-0111 to WL), and Key Project of Chinese Ministry of Education (No. 212136 to CY). We thank the Forestry Department of Guizhou Province and Kuankuoshui National Nature Reserves for support and permission to carry out this study, and J. Wu, X. Guo, X. Xu, N. Wang and L. Wang for assistance with field work.

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大杜鹃（*Cuculus canorus*）与其宿主灰喉鸦雀（*Paradoxornis alphonsianus*）的卵色模拟

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摘要：卵色多态性在大杜鹃（*Cuculus canorus*）与其宿主灰喉鸦雀（*Paradoxornis alphonsianus*）中非常明显，在同一地理种群内，大杜鹃和宿主灰喉鸦雀均分别对应出现了蓝色、浅蓝色和白色的卵。已有研究表明这很可能是两者协同进化过程中分裂选择的结果。然而，仅仅基于人眼评估的卵色分析结果是不够的，一是无法准确量化，二则由于人眼无法探测到鸟类所能感知的紫外光（UV）部分。本研究采用光纤光谱仪，量化比较了大杜鹃与其宿主灰喉鸦雀卵色的多态性及模拟程度。结果表明，光谱仪量化结果与基于人眼评估的卵色模拟情况大致吻合，同时发现大杜鹃与灰喉鸦雀二者卵色在紫外光部分也相当模拟。然而，产白色卵的杜鹃与产白色卵的鸦雀之间的模拟程度，要低于产蓝色卵的杜鹃和鸦雀。这表明，灰喉鸦雀产白色卵很可能是由于杜鹃寄生压力所导致的后进化结果。

关键词：巢寄生，卵色，卵反射度，滞后进化