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# Brood parasites lay eggs matching the appearance of host clutches

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Interspecific brood parasitism represents a prime example of the coevolutionary arms race where each party has evolved strategies in response to the other. Here, we investigated whether common cuckoos (*Cuculus canorus*) actively select nests within a host population to match the egg appearance of a particular host clutch. To achieve this goal, we quantified the degree of egg matching using the avian vision modelling approach. Randomization tests revealed that cuckoo eggs in naturally parasitized nests showed lower chromatic contrast to host eggs than those assigned randomly to other nests with egg-laying date similar to naturally parasitized clutches. Moreover, egg matching in terms of chromaticity was better in naturally parasitized nests than it would be in the nests of the nearest active non-parasitized neighbour. However, there was no indication of matching in achromatic spectral characteristics whatsoever. Thus, our results clearly indicate that cuckoos select certain host nests to increase matching of their own eggs with host clutches, but only in chromatic characteristics. Our results suggest that the ability of cuckoos to actively choose host nests based on the eggshell appearance imposes a strong selection pressure on host egg recognition.

## 1. Introduction

Mutual interactions among various animal taxa can be considered as an important selective force affecting evolutionary diversity [1]. Such reciprocity in relations is typical also of obligate brood parasitism, a life strategy used by some arachnids, insects, fishes and birds [2–5]. Obligate brood parasites are notorious for abandoning their parental duties to other species, the hosts. Because of the costs incurred on the side of the hosts, the brood parasitic breeding strategy has led to the evolution of host defences, which, in turn, have selected for more intricate counteradaptations in the brood parasite. Such an escalating arms race between brood parasites and their hosts thus represents an outstanding textbook example of coevolution [6]. This reciprocal relationship can fundamentally shape life histories, morphologies, physiologies and behaviours of both brood parasites and their hosts and influence trajectories and outcomes of their subsequent coevolutionary interactions [7]. In birds, about 1% of species have adopted the brood parasitic lifestyle [5]. The most striking adaptations by which avian brood parasites attempt to evade host defences are those related to the resemblance of host eggs, i.e. mimicry—the phenomenon that has fascinated researchers since Baldamus [8].

From the adaptive perspective, it should be beneficial for an individual brood parasite to produce progeny that will tend to exploit the same host species and evolve better tuned egg mimicry. This may consequently lead to the evolution of host-specific lineages, also called gentes [9–11], where females often lay eggs of a certain type to mimic the eggs of a particular host species [12,13]. In this respect, there is a wide variety of host specificity across different brood parasitic systems, ranging from an opportunistic host use in a majority of

parasitic *Molothrus* cowbirds [14] to strict host specificity associated with host–parasite co-speciation in African indigobirds (*Vidua* spp.) [15].

Brood parasitism by the common cuckoo (*Cuculus canorus*, hereafter cuckoo) is a system where the parasite interacts with its hosts via egg phenotype matching [16]. This is especially apparent in the evolution of various cuckoo host-specific races, which have highly polymorphic eggs that resemble the egg appearance of the preferred host species [12,17–19]. However, a considerable potential for egg phenotype matching also exists within each cuckoo gens. While cuckoo eggs sometimes closely match the appearance of the host clutch, on other occasions, they often show rather imperfect mimicry [20]. Nonetheless, the degree of egg matching is crucial for the breeding success of the brood parasite, as a good mimicry impedes effective egg discrimination by the hosts [21–24].

The cuckoo female searches for suitable nests by observing host nest-building activity from a close vantage point [5]. Then, she follows the status of several host nests to correctly time her egg laying (for details, see [25]). During the host egg-laying period, the parasitic female often visits the nests before the parasitism act [26–29], which gives her the possibility of choosing a fitting host clutch. Indeed, tracking of radio-tagged cuckoo females showed that they are capable of finding almost all nests in their territories, but eventually choose only some of them for parasitism [29]. Hence, the brood parasite could adopt the strategy of fine-tuned egg matching and select preferentially those host nests with eggs more similar to their own. This interesting hypothesis was investigated only recently, but with ambiguous results. Avilés *et al.* [30] and Cherry *et al.* [31] showed that cuckoo eggs were more similar to host clutches in naturally parasitized nests than in non-parasitized nests. However, these studies characterized the degree of egg matching by principal component analysis (PCA) based on reflectance spectrophotometry data with no respect to avian colour vision. However, Antonov *et al.* [32] used an avian vision physiological model [33,34], but did not confirm this hypothesis. In this study [32], however, the authors only compared cuckoo egg mimicry in naturally parasitized clutches and the nearest non-parasitized conspecific neighbour despite the fact that cuckoo females may find many nests in the broader neighbourhood, but parasitize only some of them [28,29]. The last two studies [24,35] compared matching of different egg morphs assessed by human evaluation and reported equivocal results.

In our study, we compensated for the methodological artefacts of the previous studies. To quantify egg mimicry more objectively, we used the method of physiological modelling of avian colour vision implemented in the program AVICOL [36], which calculates chromatic and achromatic contrasts between two colours (see §2). We did not only compare the mimicry of cuckoo eggs in naturally parasitized great reed warbler nests and their nearest non-parasitized conspecific neighbours, but we assessed cuckoo egg matching also in other host clutches that were suitable for parasitism in terms of timing. Moreover, we used a randomization approach [37] for statistical analysis, which is a very appropriate tool for the simulation of host nest choice by the brood parasite, providing intuitively interpretable results. By using these methods, we investigated whether cuckoo females target nests non-randomly within a population of a major host, the great reed warbler (*Acrocephalus arundinaceus*), to better match host clutches enhancing thereby the probability of egg acceptance. More specifically, our prediction was

that cuckoo eggs in naturally parasitized nests will match the appearance of host eggs better than they would do by chance.

## 2. Material and methods

### (a) Study area and field measurements

The study was carried out in two fishpond systems between Mutěnice (48°54' N, 17°02' E) and Hodonín (48°51' N, 17°07' E), Czech Republic, from 5 May to 23 June 2009. We systematically searched for great reed warbler nests in littoral vegetation surrounding the fishponds. A majority of them were found during nest building, and were checked daily until clutch completion. During these checks, each newly laid egg was numbered using a felt tip pen to allow its identification in the laying sequence. If a cuckoo egg was found in a nest, then the nest was considered as parasitized. The total sample used in analyses comprised 61 clutches (39 non-parasitized, 19 parasitized and three of uncertain parasitism status).

Each parasitized clutch included in the analyses was spectrophotometrically measured immediately after a cuckoo egg was detected. The remaining eggs from these clutches, as well as the non-parasitized clutches and those with uncertain status, were measured on the day after clutch completion. If the nest was parasitized twice, then we used only the first cuckoo egg in our analyses ( $n = 4$ ). We measured spectral reflectance of each egg in the range of 300–700 nm using a spectrophotometer (USB2000, Ocean Optics) under standard light conditions. To prevent nest desertion during the measurements, we temporarily exchanged host clutch with four to five great reed warbler eggs from abandoned nests. For measurements, we divided each egg into three regions across the longitudinal axis and took three measurements from each region (each covering *ca* 1 mm<sup>2</sup>). We avoided the egg poles to eliminate a possible measurement error owing to marked curvature of egg-shell surface. We also avoided extremely dark spots because they had very low reflectance and their measurements could influence mean reflectance values calculated per the whole egg surface.

During the measurements, the illuminant was a deuterium and halogen light source (DT-Mini-GS, Ocean Optics). The light was transferred to the eggshells through a quartz optic fibre (QR400-7-UV/VIS-BX, Ocean Optics), and was reflected at an angle of 45° to the surface. Data from the spectrophotometer were loaded into OOIBase 32 (Ocean Optics) software. The measurements were relative and referred to a standard white reference (WS-2, Ocean Optics) and to darkness. Reference and dark calibration were made prior to the measurement of each clutch.

### (b) Quantification of egg mimicry

As the shape of a reflectance curve need not necessarily correspond to how the signal is processed by the receiver, we analysed the reflectance data using models of avian vision [24,38]. Specifically, we used physiological models [33,34] implemented in AVICOL v. 6 [36] that reproduce bird retinal functioning and that account for nest luminosity and bird sensitivity to estimate chromatic and achromatic contrasts between the parasitic and host eggs. These models integrated information about ambient light conditions, the reflectance spectra of cuckoo and great reed warbler eggs, published information for single- and double-cone photoreceptor spectral sensitivities, photoreceptor noise and the transmission properties of avian eyes to get biologically reliable colour-matching estimates [39]. Ambient light values at nests of a typical open nester such as the great reed warbler were taken from Avilés *et al.* [40]. Sensitivity of single-cone photoreceptors was used to calculate chromatic contrasts and sensitivity of double cones to calculate achromatic contrasts [41]. Spectral sensitivity has never been measured in the cuckoo, but most bird species belong to one of two main groups differing particularly in spectral sensitivity of UV cones—UVS

(ultraviolet-sensitive) and VS (violet sensitive) group [42]. Therefore, we used data published in TetraColourSpace [43] for two representatives of each group, the blue tit (*Cyanistes caeruleus*) for UVS [44] and the Indian peafowl (*Pavo cristatus*) for VS type of colour vision [45] and conducted all statistical analyses for both types of colour vision separately. We determined the relative proportions of the different single-cone types in the retina according to available data (blue tit: ultraviolet-sensitive (UVS) single cones = 1, short-wavelength-sensitive (SWS) single cones = 1.92, medium-wavelength-sensitive (MWS) single cones = 2.68 and long-wavelength-sensitive (LWS) single cones = 2.70, derived from [44]; peafowl: UVS = 1, SWS = 1.9, MWS = 2.2 and LWS = 2.1, derived from [46]). For the high-intensity noise, we used a Weber fraction value of 0.05 in both models.

The Vorobyev–Osorio model calculates chromatic (difference in hue) and achromatic (difference in brightness) contrasts between cuckoo and great reed warbler eggs in just noticeable differences. Essentially, cuckoo eggs that appear similar to a host clutch have smaller values of both contrasts than those with poor mimicry. For further details of contrasts calculations, see [33,34,36].

### (c) Statistical analyses

Cuckoos frequently parasitize nests at the beginning of host egg laying [5] and eat up one to three host eggs before or during the parasitism event [28]. Therefore, earlier-laid host eggs may be removed preferentially in comparison with the later-laid eggs, which are usually paler [47,48]. Moreover, cuckoos could non-randomly predate on host eggs of a particular type. This could make the parasitized clutches distinct from the non-parasitized ones and influence our results. Therefore, we tested whether the naturally parasitized ( $n = 19$ ) and non-parasitized ( $n = 39$ ) host clutches differ in various characteristics of colour, such as hue, brightness and saturation. Specifically, we defined hue as relative photon catches of all four blue tit cone types involved in chromatic discrimination and brightness as blue tit double-cone photon catches [41,49]. Saturation was estimated as the distance of the point from the achromatic centre of blue tit colour space [43]. For analysis of spectral data, we used R package `P_AVO` [50,51]. All comparisons were conducted using Wilcoxon tests, because the data did not comply with normality.

To test the egg-matching hypothesis, we used a randomization test [37]. Because the evidence for exclusive territory defence of cuckoo females is equivocal [52–56] and because home-range sizes of female cuckoos vary widely between 33 and 217 ha in our study area [57], we randomized the occurrence of parasitic eggs in host clutches across the whole host population while accounting for similar timing of egg laying. Accordingly, we assigned to each cuckoo egg the host clutches that were in the laying phase on the day when the focal cuckoo egg was laid, including the naturally parasitized clutches. The laying phase was defined as a 6-day interval from the day when the first host egg was laid, because cuckoos in our population parasitize host nests most frequently during this period. As a result, between four to sixteen host clutches were assigned to each cuckoo egg, and each measured host clutch ( $n = 61$ ) was used at least once. We then calculated both chromatic and achromatic contrasts between each parasitic egg ( $n = 19$ ) and all the assigned host clutches, whereby we obtained a total of 203 chromatic and achromatic contrasts. Further, we randomly selected one contrast belonging to each cuckoo egg and calculated a mean value of these 19 contrasts. This procedure was repeated 9999 times. Finally, we sorted these 9999 mean contrasts by their values and also included the mean contrast from 19 naturally parasitized nests. According to the egg-matching hypothesis, cuckoo eggs should exhibit lower contrasts to host eggs in the naturally parasitized clutches than cuckoo eggs in randomly assigned host

clutches. To explore this scenario, we calculated the proportion of all simulated mean contrasts that were lower than the mean contrast of naturally parasitized nests. This proportion represents the significance level of the randomization test [37].

Additionally, we conducted pair-wise comparisons ( $t$ -tests) of both chromatic and achromatic contrasts of the naturally parasitized clutches with the nearest active non-parasitized clutches available for the cuckoo on the day of parasitism on the focal nest ( $n = 15$ ). The mean distance between the nearest neighbour nests was  $438.9 \pm 343.4$  m (range: 20–1068 m). All statistical calculations were performed in R v. 2.15 [51].

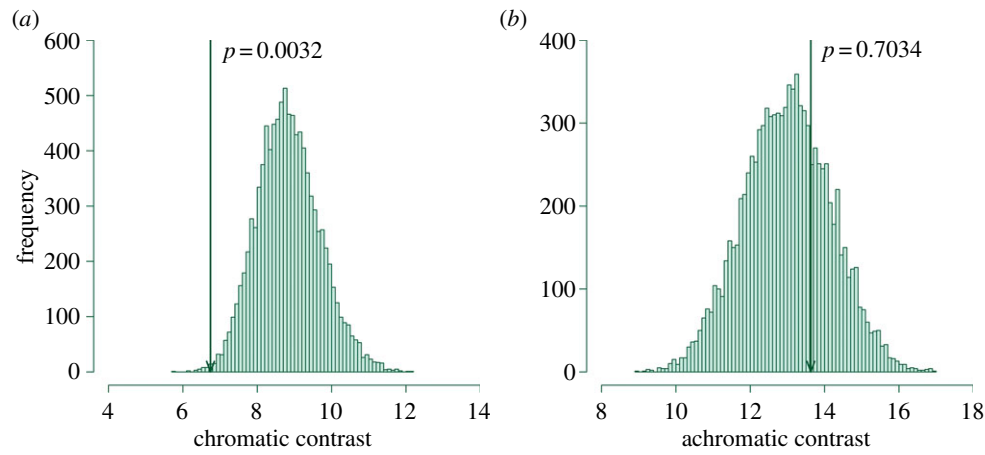
## 3. Results

There were no differences in parasitized and non-parasitized host clutches in terms of eggshell colour characteristics, such as hue, brightness and saturation (all  $p$ -values  $> 0.19$  for UVS and VS types of colour vision), and thus these differences could not influence the results of our randomization analyses.

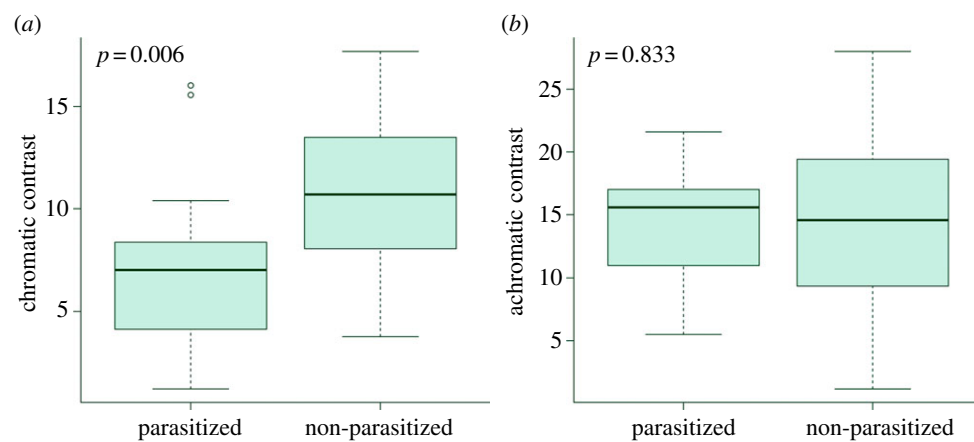
Randomization tests revealed that cuckoos did not lay their eggs into host nests haphazardly, but matched host clutches in chromatic spectral characteristics (figure 1). Significant  $p$ -values ( $p = 0.0032$  for UVS,  $p = 0.0142$  for VS) showed that only in 32 and 142 cases of 9999 runs, respectively, was the mean chromatic contrast from 19 randomly simulated clutches lower than the mean chromatic contrast calculated from the naturally parasitized clutches. On the other hand, there was no indication of achromatic matching (randomization tests:  $p = 0.703$  for UVS and  $p = 0.666$  for VS). Similarly, the comparisons between the naturally parasitized nests and their nearest non-parasitized neighbours with similar timing showed a significant difference in chromatic contrast ( $t = -3.24$ ,  $p = 0.006$  for UVS;  $t = -2.40$ ,  $p = 0.030$  for VS), but not in achromatic contrast ( $t = -0.21$ ,  $p = 0.83$  for UVS;  $t = -0.24$ ,  $p = 0.82$  for VS; figure 2). Both types of analyses give compelling evidence that the cuckoos actively select host nests for parasitism in order to match the appearance of host clutches in chromatic characteristics.

## 4. Discussion

Similar to Avilés *et al.* [30] and Cherry *et al.* [31], we found that cuckoo females probably use egg appearance as an important cue to select host nests. Although our methodological approach was different from that used in these two studies (see §2), it is interesting that we obtained quite similar results. Within a host population, cuckoo females parasitized clutches with lower chromatic contrast than their own eggs but did not use the information about the differences in achromatic eggshell characteristics. Low importance of the achromatic contrast in the great reed warbler could be explained by the nest light environment hypothesis [58–60]. This hypothesis proposes that visual signals perceived by the receiver are significantly affected by the amount of ambient light. Dim light conditions allow only scotopic or mesopic vision, and perception of colour signals is therefore strongly limited [61]. In these situations, discrimination based on achromatic contrast may be favoured [40,62,63]. However, the great reed warbler is a typical open nester, and the amount of light inside its nests most likely allows photopic vision and good discrimination of colours [61]. In such conditions, chromatic differences between two spectra are more perceptible than



**Figure 1.** Histograms of 9999 averaged (a) chromatic and (b) achromatic contrasts between cuckoo eggs ( $n = 19$ ) and all host clutches ( $n = 61$ ) with a similar egg-laying date obtained from the randomization procedure. Arrows denote positions of values of mean contrasts between cuckoo eggs and host clutches in naturally parasitized nests ( $p$ -values given). Only results for UVS bird colour vision presented. (Online version in colour.)



**Figure 2.** (a) Chromatic and (b) achromatic contrasts between cuckoo and host eggs in naturally parasitized nests and nearest non-parasitized active nests with a similar egg-laying date ( $n = 15$ ,  $p$ -values given). Only results for UVS bird colour vision presented. (Online version in colour.)

under poor light conditions [64]. Therefore, egg discrimination under such light conditions may favour chromatic rather than achromatic visual signals [33,39]. Indeed, some studies confirmed that egg-rejection behaviour in bright light conditions depends primarily on chromatic rather than on achromatic contrast [23,24,60]. Such host behaviour may create a selection pressure on the cuckoo, which can gain an advantage if it chooses the correct host clutches on the basis of the chromatic signal. And this is what we found in our study population—cuckoo females selected host clutches similar to their own eggs in chromatic features.

In contrast to the results of Avilés *et al.* [30], Cherry *et al.* [31] and the present study, Antonov *et al.* [32] did not support the egg-matching hypothesis in the closely related marsh warbler (*Acrocephalus palustris*). The authors argued that selection of better matching host egg phenotypes probably cannot exist in a host–parasite system where host inter-clutch variation is continuous, overall low or moderate. However, these traits also partly apply to great reed warbler eggs [65–67]. The discrepancy in results could be explained by different light conditions in the nesting habitats of these two warbler species. The vegetation surrounding marsh warbler nests is generally denser than in the pure reed beds used by the great reed warblers [68,69] and probably provides a different light environment, not only in terms of the quantity but also the quality of the light [70]. However, it is not apparent whether

this difference in nest light environment is sufficient to explain the differing results of the cited studies. In addition, it is also possible that the denser nesting vegetation of the marsh warbler makes the nest search more difficult for the cuckoos and prevents them from finding enough nests from which to make their selection, and the differences in nest availability between the two warbler species at the two study sites could also play a role. While Antonov *et al.* [32] claimed that the marsh warbler shows a secretive nesting behaviour and low nest density, our data on the great reed warbler demonstrate that during the peak breeding season the cuckoos have ample opportunities to choose [71].

It is interesting that our results were consistent for both main types of avian colour vision. These two groups differ primarily in the spectral sensitivity of their ultra-short-wavelength cones (UVS or VS type). The other three types of cones are relatively conservative in all bird species with certain variability in SWS cones [42,72]. Unfortunately, it is not yet known for certain whether the common cuckoo belongs to the UVS or the VS group (although some indirect evidence suggests the VS group in cuckoos; see [73,74]). However, we conducted our analyses using both types of avian colour vision, thus we are confident that any errors associated with this ‘cone sensitivity problem’ did not affect our results.

It must be pointed out, however, that our findings could be potentially biased owing to quick and thus unobserved

rejections of poorly matching parasitic eggs in nests of uncertain parasitism status ( $n = 3$ ). To be sure that this was not the case, we performed new randomizations where we added three artificially created (simulated) parasitized clutches with average chromatic contrasts to the original sample size. Detailed description of methods of these additional simulations is summarized in the electronic supplementary material. The results of these simulations showed that the addition of three simulated parasitized clutches did not affect the results of our original analysis ( $p = 0.0173$  and  $0.0311$  for UVS and VS, respectively). Moreover, the cuckoo is not only a brood parasite but it can also partially predate on host clutches without parasitizing them [75]. In addition, Moksnes *et al.* [28], who videotaped nests of the reed warbler (*Acrocephalus scirpaceus*) during egg laying, recorded cuckoo visits in 20 nests; however, only 14 of them were parasitized. The remaining six nests were only partially depredated by the cuckoo. If we apply this ratio to our data (19 parasitized nests and three nests with uncertain status), then it would suggest that some (if not all) of these three nests were most probably only partially depredated and not parasitized.

An interesting and important question is whether cuckoos really profit from the host selection in our study area. Our recent study revealed that the great reed warblers recognize parasitic eggs based on the chromatic contrast, but only in well illuminated nests [60]. However, the chromatic contrast alone (calculated for UVS type of cones) did not differ between rejecters ( $n = 16$ ) and acceptors ( $n = 23$ ; Wilcoxon test,  $W = 217$ ,  $p = 0.36$ , data from 2009 and 2010). This may be because cuckoos match the appearance of the host clutches, thus reducing the contrast perceived by the hosts. We suggest that cuckoo parasitizing host clutches similar to its own eggs in chromatic aspects may even get below the discrimination threshold of its host. By reaching the host's acceptance threshold, the brood parasite may effectively escape host rejection of parasitic eggs and thereby increase its reproductive success.

If the egg-matching scenario is true and the cuckoo females preferentially select the best-matching host nests, then they should know what their own eggs look like. A number of studies have been published on the mechanisms

of own egg recognition in cuckoo hosts [76–83] and some of them suggest that birds possess an internal template of their own eggs [81–83]. So, one may expect that cuckoos may exhibit such abilities as well. Owing to the elusive lifestyle of the cuckoo, however, the direct mechanism of how cuckoo females know the appearance of their own eggs remains enigmatic. Similar to the hosts, the memory template of their own eggs may comprise an inherited and a learned component acquired during the first egg laying [79]. The idea mentioned by Antonov *et al.* [32] that the first cuckoo egg is laid somewhere in isolation seems highly unlikely [5]. Instead, cuckoo females are probably able to remember the appearance of their own eggs and compare this self-referent phenotype with the appearance of host clutches they have visited prior to laying. However, to the best of our knowledge, the cuckoo has never been observed watching its egg during the very short parasitism events.

The main conclusion of this study is that cuckoos do not lay eggs haphazardly in a host population, but match the appearance of host clutches with respect to chromatic contrast. By doing so, they may effectively reduce the chance of egg rejection by the host and thus enhance their reproductive success. However, it is currently difficult to explain how the cuckoo can learn the appearance of its own eggs. Therefore, we highly encourage others to test this appealing idea in future studies.

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**Data accessibility.** Data are deposited in the Dryad repository: doi:10.5061/dryad.5m400.

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