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COVER PHOTO: In the coevolutionary arms race between the common cuckoo (*Cuculus canorus*) and its hosts, cuckoos have evolved eggs (top) that are often a very close match in appearance to those of their target hosts (bottom). The cuckoo's total mismatch (far right) to the immaculate blue egg of the dunnock (*Prunella modularis*) is a glaring exception which exists because this host does not reject foreign eggs. See pages 2004–2013. Photos: Mary Caswell Stoddard © NHM.

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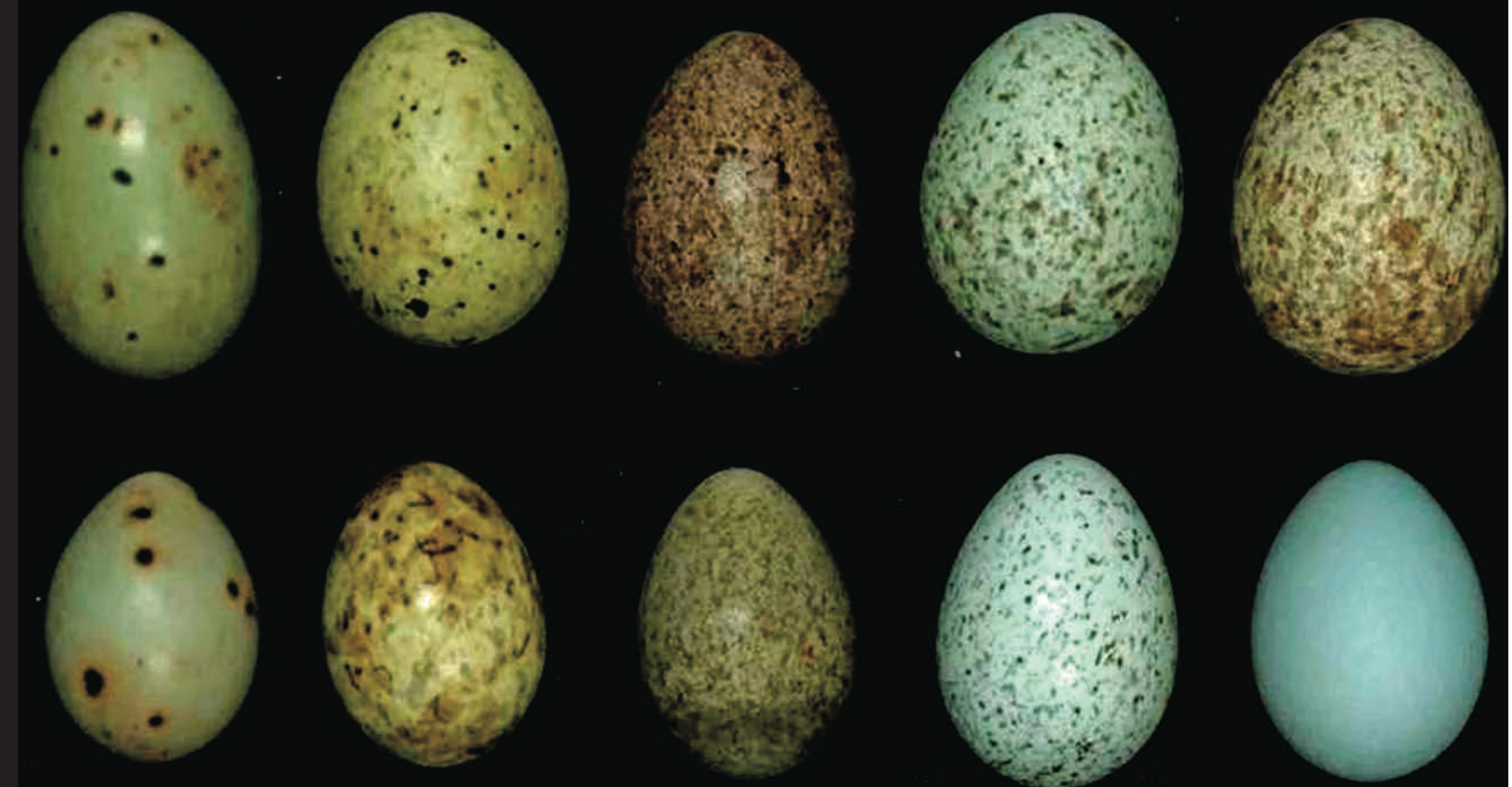
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effects under parent-offspring
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AVIAN VISION AND THE EVOLUTION OF EGG COLOR MIMICRY IN THE COMMON CUCKOO

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Coevolutionary arms races are a potent force in evolution, and brood parasite–host dynamics provide classical examples. Different host-races of the common cuckoo, *Cuculus canorus*, lay eggs in the nests of other species, leaving all parental care to hosts. Cuckoo eggs often (but not always) appear to match remarkably the color and pattern of host eggs, thus reducing detection by hosts. However, most studies of egg mimicry focus on human assessments or reflectance spectra, which fail to account for avian vision. Here, we use discrimination and tetrachromatic color space modeling of bird vision to quantify egg background and spot color mimicry in the common cuckoo and 11 of its principal hosts, and we relate this to egg rejection by different hosts. Egg background color and luminance are strongly mimicked by most cuckoo host-races, and mimicry is better when hosts show strong rejection. We introduce a novel measure of color mimicry—“color overlap”—and show that cuckoo and host background colors increasingly overlap in avian color space as hosts exhibit stronger rejection. Finally, cuckoos with better background color mimicry also have better pattern mimicry. Our findings reveal new information about egg mimicry that would be impossible to derive by the human eye.

KEY WORDS: Arms race, brood parasitism, bird color space, coevolution, egg rejection, tetrachromatic.

Coevolutionary dynamics between brood parasites and hosts can result in antagonistic arms races or stable equilibria (Davies 2000; Svensson and Råberg 2010). Interactions between the common cuckoo, *C. canorus*, and its hosts provide a classical example of an evolutionary arms race, in which most hosts have evolved egg rejection behavior. Selection pressure imposed by parasitism leads to strong host adaptations to detect and reject foreign eggs and to parasite counter-adaptations, including egg mimicry (Dawkins and Krebs 1979; Rothstein 1990). The battle at the egg-laying stage is critical because if the host fails to reject a parasitic egg, it loses all offspring to the parasite and rears only the foreign cuckoo chick (Davies 2000). Darwin (1872) and Wallace (1889) both remarked on the sophisticated egg color mimicry achieved by cuckoos, and many studies since have investigated the degree of egg mimicry between brood parasites and hosts (e.g., Brooke and Davies 1988; Davies and Brooke 1989; Moksnes and Røskoft 1995). The majority of these studies relied on human vision, yet humans have impoverished color vision compared to birds

(Goldsmith 1990; Bowmaker et al. 1997; Hart 2001a; avian color vision reviewed in Cuthill 2006). Unlike humans, birds have a fourth single cone in their retinas that is sensitive to ultraviolet (UV) wavelengths (reviewed in Hart 2001a; Cuthill 2006). Furthermore, birds have double cones that are thought to play a key role in achromatic tasks related to texture and pattern (Jones and Osorio 2004). Although various other studies have used reflectance spectra to quantify egg mimicry objectively (e.g., Starling et al. 2006; Cherry et al. 2007), spectra do not reveal how the signal is processed by the bird's receptors and color channels. Spectrometry fails to use the full range of techniques available to model receiver vision and at times may even produce misleading results (see e.g., Cassey et al. 2009; Higham et al. 2010).

Recent advances in our understanding of avian vision make it possible to evaluate egg mimicry in a way that is relevant to the signal receiver (i.e., hosts). Avian perceptual modeling has been incorporated in several new studies with great success, indicating that egg-rejection behavior is more accurately predicted

when eggs are studied from the bird visual perspective (e.g., Avilés 2008; Cassey et al. 2008; Spottiswoode and Stevens 2010). Cassey et al. (2008) showed that rejection of painted eggs by song thrushes (*Turdus philomelos*) was predicted by an avian perceptual model incorporating information from UV- and short wavelength-sensitive cones. Avilés (2008) used perceptual modeling to quantify chromatic and achromatic matching between eggs of six races of the common cuckoo *C. canorus* and two cavity-nesting hosts in Finland: the redstart (*Phoenicurus phoenicurus*) and pied wagtail (*Motacilla alba*). Avilés found that eggs of redstarts and parasitic *Phoenicurus*-cuckoos are perceptually similar, which may explain why few *Phoenicurus*-cuckoo eggs are rejected by redstart hosts. More recently, egg rejection experiments and modeling of avian color and pattern vision with the African cuckoo finch (*Anomalospiza imberbis*) and its main host the tawny-flanked prinia (*Prinia subflava*) have shown that prinia use multiple independent pattern and color cues when deciding whether to reject a foreign egg (Spottiswoode and Stevens 2010).

Previously, we documented the degree of pattern mimicry between the common cuckoo and eight of its principal hosts in Europe in terms of bird vision and showed that when host rejection was higher, cuckoo eggs matched host eggs more closely for a range of independent pattern attributes, including marking size, dispersion, contrast, egg coverage, and variation in marking size (Stoddard and Stevens 2010). However, that study did not analyze the color or luminance of either the egg background or markings. Here, we use a visual discrimination model to quantify egg color and luminance mimicry between the common cuckoo and 11 main European hosts, for both egg background and spots, to determine how difficult (on average) it would be for a host parent to detect a cuckoo egg. In addition, we model the distributions of cuckoo and host egg colors in avian tetrachromatic color space (Endler and Mielke 2005; Stoddard and Prum 2008), which provides a novel way of visualizing egg color mimicry. Following Stoddard and Prum (2008), we calculate the volume of cuckoo and host distributions, and we introduce a powerful new measure (“color overlap”) to describe the overlapping volume of cuckoo and host colors. Quantifying color overlap reveals how closely the range of possible cuckoo egg colors corresponds to the range of host egg colors in terms of avian vision. Finally, it is often argued that the level of mimicry of host eggs achieved by a cuckoo is an outcome of the selection pressure hosts place on cuckoos by rejecting foreign eggs (both in terms of intensity and the amount of evolutionary time both parties have been coevolving). We therefore evaluate the extent to which color mimicry is explained by host rejection rates reported in the literature (Avilés and Garamszegi 2007). We link our current findings to previous work investigating pattern mimicry by common cuckoos to determine if cuckoos with more effective color mimicry also tend to have more ef-

fective pattern mimicry (Stoddard and Stevens 2010). Although this outcome may seem intuitive, it is by no means certain given that color and a range of pattern attributes have previously been shown to be uncorrelated and used independently in egg rejection in other systems (Spottiswoode and Stevens 2010).

Methods

DATA COLLECTION

We obtained reflectance spectra from cuckoo and host eggs in 248 parasitized clutches held in the Natural History Museum (NHM; Tring, Hertfordshire, UK), with clutches belonging to 11 principal cuckoo hosts in Europe: great reed warbler (*Acrocephalus arundinaceus*, $n = 25$), meadow pipit (*Anthus pratensis*, $n = 16$), reed warbler (*Acrocephalus scirpaceus*, $n = 25$), sedge warbler (*Acrocephalus schoenobaenus*, $n = 15$), robin (*Erithacus rubecula*, $n = 26$), brambling (*Fringilla montifringilla*, $n = 14$), red-backed shrike (*Lanius collurio*, $n = 25$), pied wagtail (*M. alba*, $n = 25$), dunnoek (*Prunella modularis*, $n = 27$), redstart (*P. phoenicurus*, $n = 24$), and garden warbler (*Sylvia borin*, $n = 26$). The majority of eggs were collected between 1880 and 1910 in several European countries (Supporting Information: Data collection). To avoid pseudoreplication (measuring multiple cuckoo eggs laid by the same female), we used clutches from different localities, or, when this was not possible, clutches acquired several years apart or by different collectors. For each parasitized clutch, we measured one cuckoo egg and one randomly selected host egg.

SPECTRAL MEASUREMENTS OF EGGS

We obtained reflectance spectra for each egg using an Ocean Optics USB4000 spectrometer (Dunedin, FL) with illumination by a PX-2 pulsed Xenon lamp. We used a narrow-ended (1/8") probe held at a constant distance and a 45° angle to the egg surface to measure reflectance at the top, middle, and base of the egg. Two measures (one background, one spot) were taken from each egg region, recorded at 1-nm intervals from 300 to 700 nm, expressed relative to a Spectralon™ 99% white reflectance standard (Lab-sphere, Congleton, UK), and then averaged across egg region to yield one mean background spectrum and one mean spot spectrum per egg (Fig. S1). For the meadow pipit and its respective cuckoo host-race (gens), eggs are so densely spotted that only two background and two spot measurements were possible per egg. For the sedge warbler and its respective cuckoo host-race, eggs are almost uniformly covered with “spots,” so one measurement (including portions of “background” and “spot”) was taken per egg region and subsequently averaged. Eggs of the great reed warbler and its cuckoo have dark and light spots; for these eggs, two dark and two light spots were measured per egg.

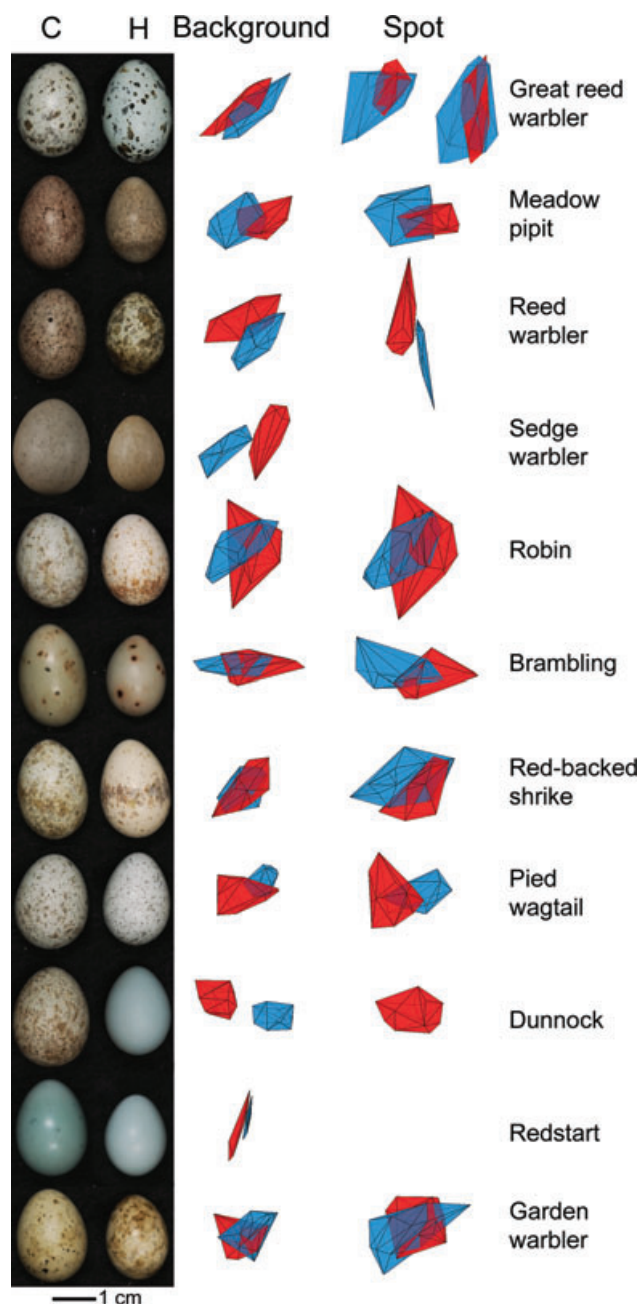


Figure 1. Photographs of cuckoo (left) and host (right) eggs are shown with their background and spot color distributions in avian tetrahedral color space, illustrating the extent of color overlap between cuckoos (red) and hosts (blue). Distributions have been enlarged from their original positions in the tetrahedral color space and are all shown on the same scale, except for the light spot (left) and dark spot (right) distributions for great reed warbler, shown at 50%. Distributions have been rotated around the vertical axis to better show regions of overlap. Eggs of the sedge warbler and its cuckoo were so densely covered with spots that only one color (including portions of background and spot) was measured, shown here as the background color. Photographs of eggs within the figure are copyright of the NHM and UMZC (sedge warbler-cuckoo and sedge warbler eggs) and were taken by Mary Caswell Stoddard.

MODELING AVIAN QUANTAL (PHOTON) CATCHES AND DISCRIMINATION

To determine how well cuckoo eggs matched those of their hosts, we quantified the difference in avian color and luminance perception. Two classes of color vision exist in birds, in which the fourth color cone uses UV-sensitive (UVS) or violet-sensitive (VS) opsin pigments (reviewed in Cuthill 2006). Except for Corvidae, Tyrannidae, and Meliphagidae, passeriformes are thought to have UVS-type cones (Ödeen and Håstad 2003, 2010). Therefore, to estimate how eggs appear to passerine hosts, we used average egg spectra to model the photon catches of the single and double cones of a blue tit *Cyanistes caeruleus* (Hart et al. 2000). The red-backed shrike (*L. collurio*) belongs in the family Laniidae, which is closely related to VS Corvidae (Barker et al. 2004; Hackett et al. 2008). It has not yet been determined in any Laniidae species whether the UVS or VS visual type prevails. To account for any error associated with misattributing the visual system in this species, we repeated discrimination and tetrachromatic color analyses for Red-backed shrike using a VS peafowl model (Hart 2002). Color vision in birds stems from the four single cone types (reviewed in Cuthill 2006), whereas luminance-based tasks are thought to stem from the double cones (Jones and Osorio 2004). We modeled both color and luminance discrimination using irradiance spectra collected from a UK deciduous woodland environment (Madingley Woods, Cambridgeshire) with an Ocean Optics (Dunedin, FL) cosine-corrected spectrometer. We repeated the analyses treating the irradiance spectrum as a constant with an integral equal to 1 (Stoddard and Prum 2008) and found that chromatic contrasts were strongly correlated with those calculated using woodland light ($R^2 = 0.996$), as predicted by the efficacy of the von Kries transformation and color constancy (Vorobyev et al. 1998; Stoddard and Prum 2008). Likewise, previous work modeling avian egg colors has shown that using different irradiant light spectra has a minimal influence on modeled photon catch values (Langmore et al. 2009).

To determine color contrasts, we calculated the discriminability of cuckoo and host eggs according to the log form of the Vorobyev and Osorio (1998) receptor noise model. We used a Weber fraction value of 0.05 (for the most abundant cone type), and relative proportions of cone types in the retina for a blue tit (longwave = 1.00, mediumwave = 0.99, shortwave = 0.71, and UVS = 0.37; Hart et al. 2000). Cone abundance ratios can vary substantially between species (Hart 2001b) and may lead to differences in color discrimination (Lind and Kelber 2009); unfortunately the relative cone proportions have not yet been determined for any of the species in this study and are only known for a handful of birds (Hart 2001b). For modeling red-backed shrike colors with VS sensitivity, we retained blue tit cone proportions rather than using very similar data for peafowl (longwave = 0.96, mediumwave = 1.00, shortwave = 0.85, UVS = 0.46, Hart 2001b),

which are not necessarily more similar to red-backed shrike than are data for blue tit. We used blue tit cone ratios consistently throughout the study to ensure that differences we detected were due to differences in color sensitivity rather than relative cone abundances and noise levels. To model luminance discrimination, we followed Siddiqi et al. (2004) in calculating the difference between two stimuli for the double cones. The results of these models are expressed in “just noticeable differences” (JND), where generally a JND of less than 1.00 indicates that two stimuli are indistinguishable, with values increasing above 1.00 indicating more rapid discrimination (Siddiqi et al. 2004). For each cuckoo egg, we calculated the chromatic and achromatic contrasts (JND) between every available host egg for that species and used the mean chromatic and achromatic contrasts in subsequent analyses.

MODELING RECEPTOR STIMULATION IN TETRAHEDRAL COLOR SPACE

We analyzed the relative cone stimulation of avian reflectance spectra in tetrahedral color space (Goldsmith 1990; Endler and Mielke 2005), using TETRACOLORSPACE with MATLAB 7 (Stoddard and Prum 2008). Avian tetrahedral color space provides a convenient, quantitative representation of bird color based on well-established cone-type sensitivities. It is not identical to a bird’s true sensory experience, which likely involves opponent mechanisms, color categorization, and complex psychophysical processing. Until much more is known about these complicated processes in birds, tetrahedral color space allows us to describe avian colors in a straightforward way that is relevant to bird vision and makes fewer assumptions than more complex models. Photon catch values of eggs were normalized to sum to one and converted to a point in color space with X, Y, and Z coordinates (Endler and Mielke 2005), with this position in the color space determined by the relative stimulation of the four color cone types. For each cuckoo host-race and host species, all egg colors were plotted as points in the tetrahedral color space and overall color space occupancy was quantified using MATLAB’s “convhulln” (Stoddard and Prum 2008). The volumes of each cuckoo and host distribution provide a measure of intraspecies color variation. A new measure (“color overlap”) was developed to describe the extent to which cuckoo and host color distributions overlap. Given that an individual cuckoo parasitizes multiple host nests, quantifying color overlap is useful for considering how well a cuckoo egg matches a host egg on average: given a particular cuckoo egg, what is the likelihood that it falls within the range of host egg colors? Color overlap is expressed as the percentage of the host volume overlapped by the cuckoo volume. This was estimated using a Monte Carlo simulation; determining an exact solution was not possible given the complexity of intersecting convex polyhedra. For each simulation, we generated a sphere of 750,000 random points in

tetrahedral color space around the center of the cuckoo and host distributions, so that both distributions were completely encompassed. We then determined the volume of random points that fell inside both the cuckoo and host volumes (the estimated color overlap; see Supporting Information: Calculating color overlap).

In avian tetrahedral color space, each egg color can be defined by a vector. Hue is defined as the direction of the color vector and is described by angles θ and ϕ , which are analogous to longitude and latitude. Chroma, or saturation, is given by the magnitude of r , or its distance from the achromatic origin (Fig. S2). Hue and saturation were characterized for all eggs, and average color span, average hue disparity, and volume were measured for all egg distributions (Table S1; and see Stoddard and Prum 2008). We used Robinson projections to analyze the hue distributions of egg colors independently of saturation (Fig. S3). Egg colors can be projected onto a sphere centered at the achromatic origin of the tetrahedron; the Robinson Projection is a two-dimensional projection of the sphere (commonly used as a representation of the earth’s surface).

COMPARISON WITH REJECTION RATES

We compared overall background and spot color mimicry to previously established rejection rates of nonmimetic eggs by hosts. Rejection rates vary widely and depend on parasitism rates and host experience (Davies 2000); we therefore refer to rates determined directly by Davies and Brooke (1989) in the Supporting Information, but here we primarily use rates calculated from published and unpublished sources compiled in Avilés and Garmszegi (2007), as only this study includes rejection rates for all species analyzed here. In our analyses, we have treated each species as an independent datapoint rather than controlling for phylogeny. Kilner (2006) demonstrated that evolutionary history is unlikely to have imposed much constraint on the evolution of egg appearance by cuckoo hosts; regardless of their evolutionary history, hosts can counter attacks by brood parasites by changing their egg coloration.

COMPARISON WITH PATTERN MIMICRY

We compared color mimicry (in terms of JND) with five pattern variables (marking size, diversity in size, contrast, coverage, and dispersion) measured for the eight species analyzed in Stoddard and Stevens (2010). For each cuckoo-host pair, we plotted color mimicry against the number of matching pattern attributes to determine whether cuckoos with better color mimicry also achieve better pattern mimicry.

Results

Distributions of cuckoo and host colors, for both the egg background and spots, illustrate the extent of overlap in avian

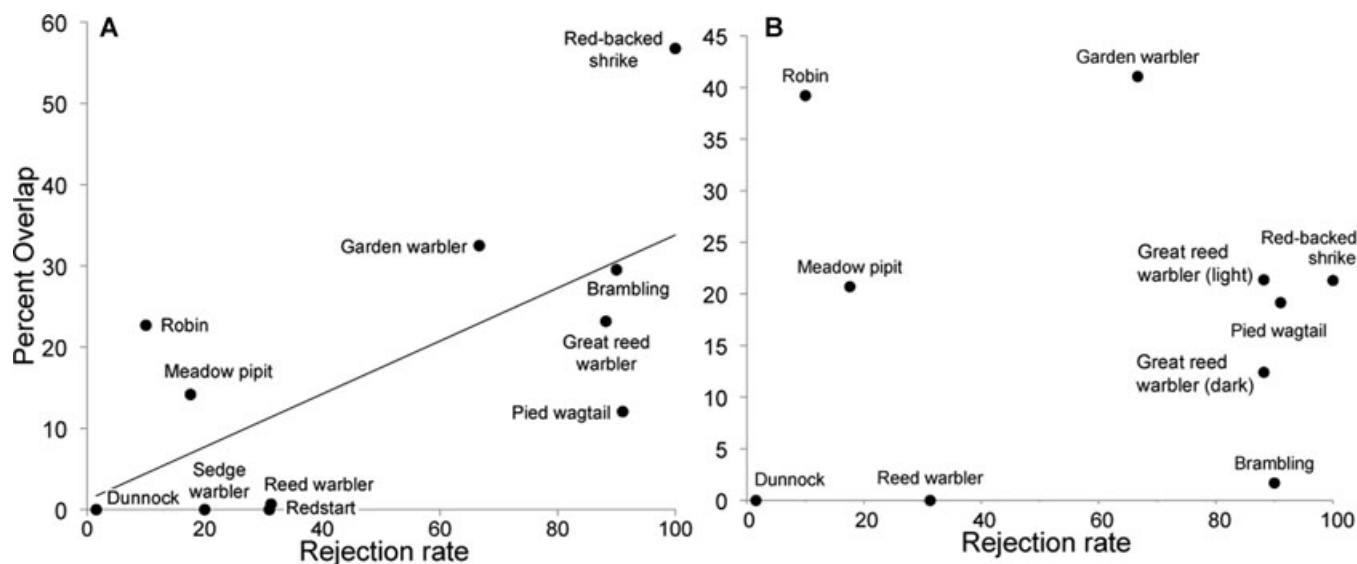


Figure 2. The relationship between host rejection rate of nonmimetic eggs and color overlap for (A) background and (B) spot colors. Color overlap is expressed as the percentage of the host volume overlapped by the cuckoo volume. Rejection rates are taken from Avilés and Garamszegi (2007).

tetrahedral color space (Fig. 1). Background color overlap, or the percent overlap of host background colors by cuckoo colors, is correlated with rejection rate ($R^2 = 0.4678$, $P = 0.02$, linear regression, Fig. 2A). Spot color overlap is not correlated with rejection rate ($R^2 = 0.0009$, $P = 0.93$, linear regression, Fig. 2B). In terms of mean discrimination values (JND), mimicry of background egg color improves where hosts show strong rejection ($R^2 = 0.6781$, $P < 0.01$, logarithmic regression, Fig. 3A). Improvement in color match with rejection becomes less pronounced as colors become close to indistinguishable ($JND < 2.5$; Fig. 3A). Luminance mimicry of the egg background improves moderately as hosts become more discriminating ($R^2 = 0.3004$, $P = 0.08$, linear regression, Fig. 3B). Neither spot color nor luminance mimicry is related to host rejection (color: $R^2 = 0.0017$, $P = 0.91$, linear regression, Fig. 3C; luminance: $R^2 = 0.0100$, $P = 0.78$, linear regression, Fig. 3D). These results were unchanged when we removed sedge warbler and its cuckoo, for which we did not obtain separate background and spot color spectra, from the analysis. A comparison of background color mimicry (JND) to the number of matching pattern attributes for eight species (measured in Stoddard and Stevens 2010) shows that cuckoos with better color matching also achieve more sophisticated pattern matching (Fig. 4). Reflectance spectra (Fig. S1) and Robinson projections (Fig. S3) further document the degree of color and luminance mimicry.

We repeated JND and tetrachromatic color analyses for the red-backed shrike and its cuckoo using a VS peafowl model. Compared to UVS vision, the relative photon catch values of egg background colors modeled with VS vision differed by less than 0.03 in each of the cone channels. For spot color photon

catches, modeling with VS vision changed photon catches by less than 0.02. Under the UVS model, the cuckoo achieves a 1.75 JND match to red-backed shrike background color and a 2.43 JND match to spot color. Under the VS model, the cuckoo-host background color difference is 1.31 JND and spot difference is 2.07 JND. For more detailed results, see Supporting Information: Background color mimicry as it relates to rejection rate.

Discussion

Here we have used avian visual modeling to quantify egg background and spot mimicry for color and luminance between the common cuckoo and 11 European hosts. Our results show that background appearance is strongly mimicked by most cuckoo host-races, with the best color and luminance matches achieved by cuckoos parasitizing hosts with strong rejection (Figs. 2A and 3A,B). Unlike background, spot mimicry for color or luminance is not strongly related to host rejection rates (Figs. 2B and 3C,D), suggesting that the pattern of spots may be more important for successful egg mimicry than the color of spots. Analysis of cuckoo and host egg colors in avian tetrahedral color space reveals that some cuckoo distributions prominently overlap those of their hosts, whereas others remain completely isolated in color space (Fig. 1). Mapping egg colors in avian tetrachromatic space revolutionizes our understanding of mimicry by capturing color variation and by illustrating which regions of color space are occupied by cuckoos and hosts. We employ a powerful new measure, color overlap, to complement discrimination modeling as a measure of color mimicry, and we advocate its use in future

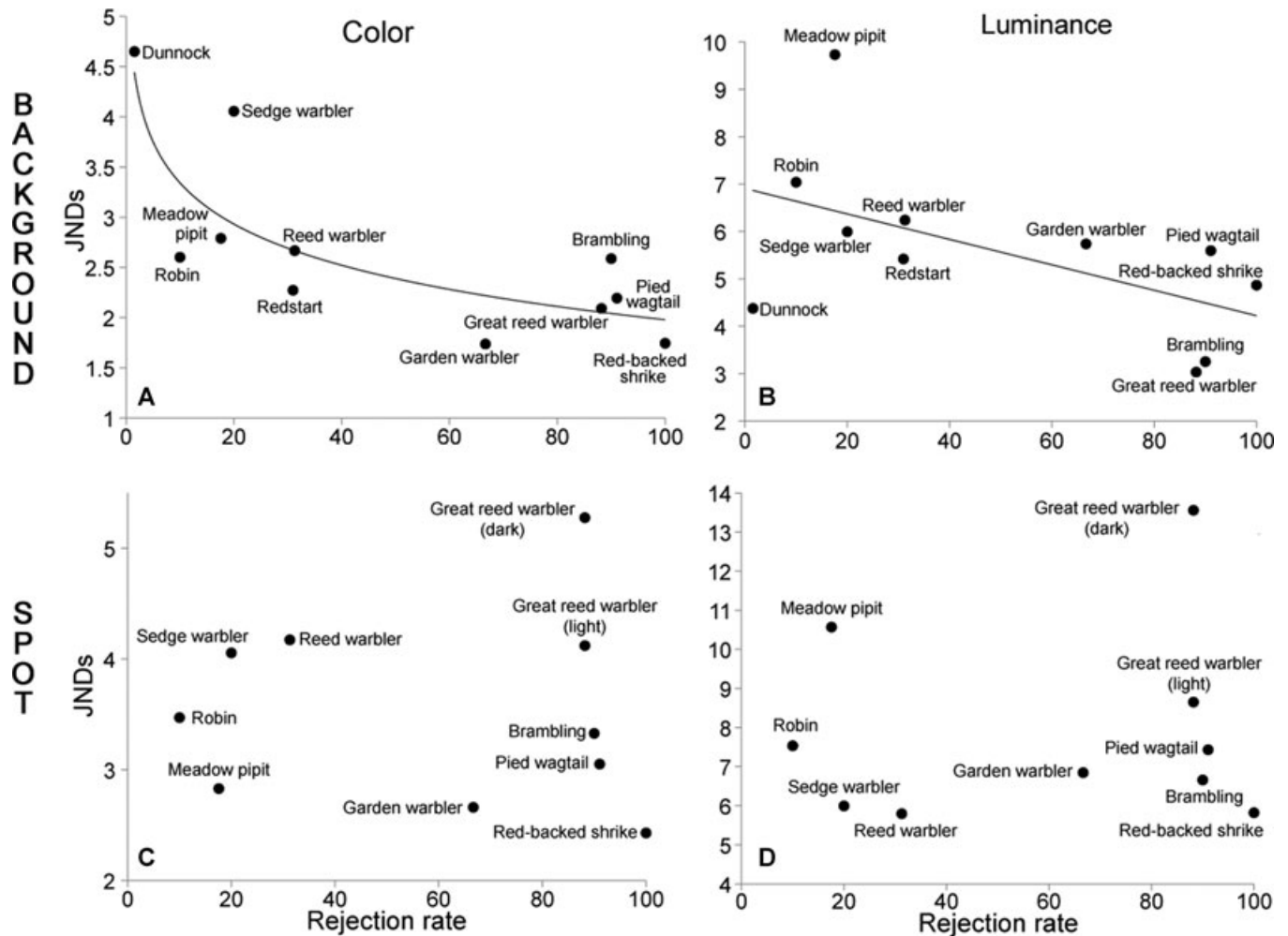


Figure 3. The relationship between host rejection rate of nonmimetic eggs and mean “just noticeable differences” (JND) between cuckoo and host eggs in terms of (A) background color, (B) background luminance, (C) spot color, and (D) spot luminance. Rejection rates are taken from Avilés and Garamszegi (2007).

studies of avian color. Both approaches provide support for the conclusion that cuckoos have evolved better background, but not spot, color mimicry to evade the most discerning hosts. As with background color, egg pattern mimicry improves as hosts show stronger rejection (Stoddard and Stevens 2010). We show for the first time that cuckoos with better background color mimicry also have better pattern mimicry (Fig. 4).

Classical work on egg polymorphisms of the common cuckoo indicated that cuckoos and hosts are at various stages of a co-evolutionary arms race (Brooke and Davies 1988; Davies and Brooke 1989). Our color analyses reveal that cuckoos lay a better matching egg where the host species is more discriminating; this is particularly true for background color mimicry and, in a previous study, for pattern too (Stoddard and Stevens 2010). The dunno-cuckoo egg, which is white with brown speckling (to human eyes), is a poor match to the immaculate blue dunno egg. Accordingly, the background colors of the dunno-cuckoo and

dunno are completely isolated in avian color space and should be discriminable (Fig. 1). Despite the obvious color mismatch, dunno readily accept foreign eggs and are thought to be at an early stage of the co-evolutionary arms race, having not yet evolved host defenses (Davies 2000). The sedge warbler-cuckoo achieves a slightly better color match to its host, which is clearly illustrated by the close proximity (but still no overlap) of the cuckoo and host color distributions in color space (Fig. 1). Like the dunno, the sedge warbler rarely rejects nonmimetic eggs and is likely at an early stage of the arms race (Davies and Brooke 1989).

In response to the evolution of stronger host defenses, cuckoos likely developed better background color mimicry. Where hosts show modest rejection, as in the robin, meadow pipit, and reed warbler, the cuckoos generally achieve better background matching and increased overlap of host colors (Figs. 1, 2A, and 3A). Redstarts also show modest rejection, and indeed the redstart-cuckoo achieves a decent color match on average to

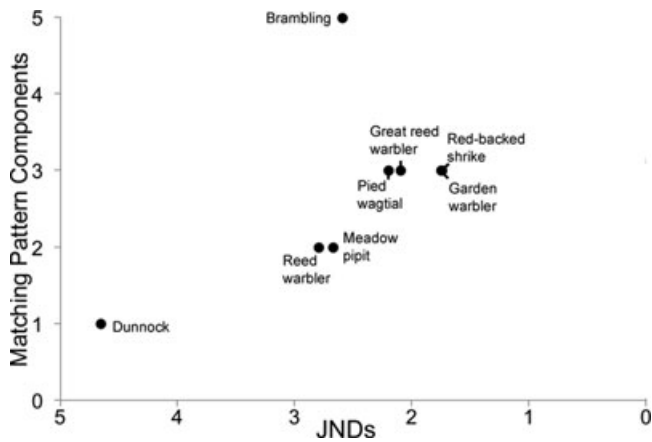


Figure 4. The relationship between color mimicry (expressed in “just noticeable differences”) and the number of matching pattern attributes (out of five) for the eight species analyzed in Stoddard and Stevens (2010). The pattern attributes were marking size, diversity in size, contrast, coverage, and dispersion. On the x-axis, color mimicry improves as JND values decrease.

host eggs (Fig. 3A). Surprisingly, however, the distribution of redstart-cuckoo background colors fails to intersect that of the host (Fig. 1). Both cuckoo and host eggs are immaculate blue and often appear mimetic to the human eye, yet there is a clear, quantifiable difference between the blue colors.

Cuckoo mimicry of background color is most impressive among hosts showing strongest rejection, including garden warbler, great reed warbler, pied wagtail, and red-backed shrike (Fig. 3A). The cuckoo that parasitizes the red-backed shrike, which is the strongest egg rejecter, achieves the highest color overlap: the cuckoo and host distributions are completely superimposed (Fig. 1), with cuckoo colors overlapping the majority of the host volume.

Surprisingly, spot color matching did not improve with host rejection rate. Although spot color matching does not relate to the discrimination ability of hosts (Figs. 2B and 3C), modeling in tetrachromatic color space indicates that spot colors are indeed mimicked (Fig. 1). All spot color distributions overlap in color space with the exception of the reed warbler and its cuckoo, where the brown spots of the cuckoo do not intersect the olive green speckling of the host (Fig. 1). This suggests that some level of spot color matching may be essential for successful mimicry, but a strong match of host spot color may be less crucial than a strong match of background color. Our previous work (Stoddard and Stevens 2010) shows that detailed aspects of pattern mimicry improve with host discrimination ability, suggesting that spot arrangement rather than spot color is critical for effective egg-copying: future egg rejection experiments could test this hypothesis directly.

Most cuckoo host-races have evolved background colors that appear highly mimetic and difficult to distinguish (i.e., with

JND < 3; Siddiqi et al. 2004). However, the tremendous variation of host rejection rate in this range and the steady improvement of background matching with increasingly strong rejection (Fig. 3A) suggest that host discrimination and cuckoo color mimicry are more nuanced and complex than previously illustrated. Interestingly, background color mimicry no longer improves as colors become very difficult to discriminate (1–2 JND). As colors become almost indistinguishable, other cues such as luminance or pattern may be preferentially used. Color tends to be used at moderate-to-high light levels, whereas achromatic information may take on a greater importance under low light (Vorobyev and Osorio 1998), including in cuckoo egg appearance (Avilés 2008; Langmore et al. 2009). We might therefore expect egg patterns (which are principally encoded by luminance) to become especially important where color cues are no longer used. Accordingly, we found that cuckoo host-races achieving the best color match (JND < 2.5; i.e., garden warbler, pied wagtail, great reed warbler, and red-backed shrike) are also those with the most sophisticated egg pattern mimicry (Fig. 4, and see Stoddard and Stevens 2010).

Our study did not include modeling of ambient light levels, which can affect the ability of a receiver to discriminate between two objects. At low light levels, such as in dark nests, discrimination ability is reduced; in addition to Weber-based receptor noise, as modeled here, noise also arises in the photoreceptors due to actual variations in photon catch (Osorio et al. 2004). It is possible that the level of mimicry in some species, such as the redstart-cuckoo, is actually better than our results imply when hosts nest in dark light conditions. Although versions of the discrimination model we used here are available for low light levels (Osorio et al. 2004; Schaefer et al. 2007; Langmore et al. 2009), at present we do not know the light level at which photon-noise becomes involved and limits discrimination; previous incorporations of photon-limited noise in models have used only rough approximations of this variable (Osorio et al. 2004; Langmore et al. 2009). Therefore, it would not have been appropriate to include this approach with our modeling, as it may have unfairly biased the level of mimicry in favor of dark-nesting species. In the future, when more is known about the psychophysics of discrimination at low light levels, modeling should be made more realistic by including such information. Further work should also investigate the light levels at which achromatic mechanisms become relatively more important than color ones for discrimination or detection, as this may be important in some cuckoo hosts with dark nests (e.g., Avilés 2008; Langmore et al. 2009). Owing to color constancy in vision and the fact that most terrestrial light environments vary relatively little (compared to marine environments, for example), it is unclear whether we expect differences in rejection behavior and the visual cues used to occur in different habitats, although this would be interesting to test.

What evolutionary mechanisms have led to excellent mimicry by cuckoos parasitizing the pickiest hosts, yet poor mimicry by cuckoos targeting less discriminating hosts? The high price of parasitism on hosts has likely led to a full-blown coevolutionary arms race, in which many hosts have evolved defenses in the form of egg detection and rejection abilities, and many cuckoo host-races have evolved highly mimetic eggs as a counter-response (Rothstein 1990; Davies 2000). Thus, host discrimination against badly matching eggs is the selective force maintaining the distinct cuckoo host-races and driving the evolution of egg mimicry. The conundrum of why many hosts accept nonmimetic eggs continues to baffle biologists: explanations for this phenomenon usually fall in two categories. Under the coevolutionary lag hypothesis, some naive hosts are still at early stages of the evolutionary arms race and so accept alien eggs, having not yet evolved defenses against parasitism (Davies 2000). Under the equilibrium hypothesis, tolerating cuckoo eggs may be the most stable strategy for some hosts if the cost of recognition errors is high and the cost of parasitism is low (Lotem et al. 1995). As an alternative to resistance, tolerance may have important and oft-overlooked implications for the coevolutionary dynamics of brood parasitism (Svensson and Råberg 2010). Both hypotheses rely on a learning process involved in host egg recognition. Hosts are thought to memorize their own egg type; they can be tricked into imprinting on the wrong egg type if their own eggs are replaced with another's during their first season (Lotem et al. 1995).

In this study, we have used host rejection rates as a proxy for the level of selection imposed by host species on cuckoos and as an estimate for the evolutionary stage that each cuckoo host-race and host species pair has reached in the arms race. In the future, it would be valuable to relate the level of color and pattern mimicry achieved by each cuckoo host-race to the amount of time they have been independently evolving (using molecular clock data and phylogenies). Unfortunately, this information is currently unavailable and recent work (Gibbs et al. 2000) indicates that cuckoo host-races have switched hosts on various occasions during their evolution.

Although the precise mechanism by which hosts detect and reject cuckoo eggs remains unclear, our analyses indicate that different hosts use different cues in egg recognition (of their own and foreign eggs) and rejection. The brambling-cuckoo, for example, has the best pattern mimicry (all five matching pattern elements, Fig. 4) and good luminance mimicry (Fig. 3B), but not a high match to host background color (Fig. 3A). For the brambling, pattern or luminance cues may provide critical signature information for egg discrimination, making a perfect background color match by the brambling-cuckoo less important. Recent evidence from hosts of the African cuckoo finch indicates that multiple cues are used to reject foreign eggs, with color and pattern each contributing approximately 50% of the visual cues used in rejection

decisions (Spottiswoode and Stevens 2010). However, the relative significance of color, luminance, and pattern cues in discrimination tasks—and the extent to which they may have coevolved—is largely unknown in hosts of the common cuckoo. Our results here, and in our previous study of pattern mimicry (Stoddard and Stevens 2010), reveal remarkable nuance and complexity of egg color and pattern, in terms of mimicry and host discrimination. This raises the intriguing question of why both color and pattern mimicry, in many cases, have evolved to be exceptional, while other seemingly obvious cues (to human eyes) like egg shape and size do not seem to be readily mimicked by cuckoos or used by hosts (but see Marchetti 2000 for an exception). One possibility is that the physical challenges of modifying egg size and shape may prohibit these forms of mimicry. Color and pattern may be more flexible traits, liberated from constraints on body size and oviduct morphology. However, coevolutionary interactions have clearly influenced egg traits beyond color and pattern: for example, cuckoos facing the fiercest host rejection have evolved thicker eggshells to resist rejection by puncture (Spottiswoode 2010). The poor ability of cuckoos to mimic egg size and shape is puzzling, but more curious is why hosts neglect to use these apparently straightforward cues when making rejection decisions. Perhaps hosts' excellent capacity for color and pattern recognition precludes the need for attention to size- and shape-based cues. Alternatively, hosts may fail to reject large eggs because the cost of making a recognition error is high. If large eggs result from greater investment, the host risks ousting its best egg by mistake. Clearly, much more work is required to better understand the evolutionary mechanisms underlying egg mimicry, including rigorous egg rejection experiments to disentangle exactly which cues are used by various hosts to detect foreign eggs.

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Supporting Information

The following supporting information is available for this article:

Figure S1. Reflectance spectra of cuckoo and host background and spot colors.

Figure S2. A tetrahedral avian color space (reproduced from Stoddard and Prum 2008).

Figure S3. Robinson projections of egg (A) background and (B) spot colors illustrate the distributions of cuckoo and host hues independent of their saturation.

Table S1. Summary statistics describing cuckoo and host egg colors (background and spot).

Table S2. Estimated and corrected color overlap values for background and spot distributions.

Supporting Information may be found in the online version of this article.

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