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Egg colour matching in an African cuckoo, as revealed by ultraviolet-visible reflectance spectrophotometry

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Despite major differences between human and avian colour vision, previous studies of cuckoo egg mimicry have used human colour vision (or standards based thereon) to assess colour matching. Using ultraviolet-visible reflectance spectrophotometry (300–700 nm), we measured museum collections of eggs of the red-chested cuckoo and its hosts. The first three principal components explained more than 99% of the variance in spectra, and measures of cuckoo–host egg similarity derived from these transformations were compared with measures of cuckoo–host egg similarity estimated by human observers unaware of the hypotheses we were testing. Monte Carlo methods were used to simulate laying of cuckoo eggs at random in nests. Results showed that host and cuckoo eggs were very highly matched for an ultraviolet versus greenness component, which was not detected by humans. Furthermore, whereas cuckoo and host were dissimilar in achromatic brightness, humans did not detect this difference. Our study thus reveals aspects of cuckoo–host egg colour matching which have hitherto not been described. These results suggest subtleties and complexities in the evolution of host–cuckoo egg mimicry that were not previously suspected. Our results also have the potential to explain the longstanding paradox that some host species accept cuckoo eggs that are non-mimetic to the human eye.

Keywords: egg coloration; cuckoos; reflectance spectrophotometry; avian colour vision; brood parasitism; mimicry

1. INTRODUCTION

Nest parasitism by cuckoos and cuckoo–host egg mimicry provide textbook examples of coevolutionary processes. It is generally thought that selection for cuckoo eggs to match those of their hosts requires hosts to distinguish cuckoo eggs from their own, leading to improved egg mimicry by the cuckoo, and improved egg discrimination by the host (Davies & Brooke 1988). A major puzzle is why so many hosts accept non-mimetic eggs and current debate on this issue has focused on two alternative explanations (Davies 1999; Winfree 1999). The first is that acceptor hosts accept non-mimetic eggs because hosts are naive, on account of being at the start of an evolutionary interaction (the coevolutionary lag hypothesis). The second alternative is that host acceptance is at an equilibrium, as rejection costs for some hosts are sufficiently high and parasitism costs sufficiently low for acceptance of cuckoo eggs to be the best option (the equilibrium hypothesis).

Here we provide evidence for a third hypothesis. This posits that host–cuckoo egg discrimination and, consequently, matching are performed only with certain combinations of wavelengths—due perhaps to hard-wiring of the host's visual system, light environments at the nest or other environmental factors, such as diet, which could co-affect the colour of eggs of both host and cuckoos living in the same locality. Consequently, selection for host–cuckoo egg matching could result in egg mimicry at only certain combinations of wavelengths. In this way, cuckoo eggs that appear non-mimetic to humans could be perceived as a good match by their avian hosts, or eggs could be matching in ways not visible to human vision.

A number of studies have indicated that visual cues are of critical importance to hosts in discriminating between their own eggs and those of brood parasites (e.g. Brooke & Davies 1988; Davies & Brooke 1988; Stokke *et al.* 1999). The fact that human colour vision differs substantially from that of birds has recently been recognized in evolutionary and ecological studies, yet no studies have measured egg coloration independently of human colour vision. Most birds are sensitive to near-ultraviolet wavelengths to which humans are blind (reviewed by Bennett & Cuthill 1994; Bennett *et al.* 1994). Birds also have at least four spectrally distinct cone types (Bowmaker *et al.* 1997), as opposed to three in humans, implying that birds probably have tetrachromatic, and even possibly higher-dimensional, colour vision (Thompson *et al.* 1992; Bennett *et al.* 1994). In addition, avian cone cells contain light-absorbing oil droplets, which act as cut-off filters, reducing the overlap between cone spectral sensitivities (Goldsmith *et al.* 1984; Partridge 1989; Bowmaker 1991; Vorobyev *et al.* 1998). Consequently, the assumption that birds see colours in the same way as humans, which has been implicit in much earlier work on sexual selection (Bennett *et al.* 1994), and which is implicit in all earlier studies of cuckoo–host egg mimicry, may be invalid. Recent experiments further reinforce the need to measure colour over the bird visible spectrum as they show that a variety of species use ultraviolet (UV) wavelengths in mate choice (Bennett *et al.* 1996, 1997; Andersson & Amundsen 1997; Hunt *et al.* 1997, 1998; Andersson *et al.* 1998) and foraging decisions (Church *et al.* 1998; Viitala

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Table 1. *Clutches of cuckoo and host eggs measured*

species	clutch	gens	number of host eggs	mean human dissimilarity score
Cape robin (*Cossypha caffra*)	1	1	2	3.9
	2	1	1	4.7
	3	3	2	2.6[a]
	4	1	2	4.8
	5	1	2	4.5
	6	1	2	4.4
	7	1	1	3.3
kurricane thrush (*Turdus libonyanus*)	1	2	2	1.6[a]
	2	1	1	4.3
	3	3	1	3.5
	4	1	2	3.3
black flycatcher (*Melaenornis pammelaina*)	1	1	2	4.8
Heuglin's robin (*Cossypha heuglini*)	1	1	2	1.4[a]
black-headed weaver (*Ploceus melanocephalus*)	1	3	1	2.6[a]
whitethroated robin (*Cossypha humeralis*)	1	1	2	3.6
	2	1	2	3.1
Natal robin (*Cossypha natalensis*)	1	1	2	1.7[a]
Cape rock thrush (*Monticola rupestris*)	1	1	2	4.9
	2	1	1	4.5
chorister robin (*Cossypha dichroa*)	1	1	1	1.0[a]
stonechat (*Saxicola torquata*)	1	1	3	4.4

[a] Values that can be classified as mimetic by humans, i.e. with a dissimilarity score of 1–3. Gens 1 is uniform chocolate-brown; gens 2 is pale blue with pinkish-brown freckling; gens 3 is pale brown with brown freckling.

et al. 1995). Whereas several studies have investigated the implications of human–bird differences in colour vision for assessments of avian sexual dichromatism (Andersson *et al.* 1998; Cuthill *et al.* 1999; Hunt *et al.* 1998; Langmore & Bennett 1999), none has yet investigated their implications in assessments of avian egg mimicry.

The red-chested cuckoo *Cuculus solitarius* is endemic to Africa and is found over most of the sub-Saharan region, with well-substantiated records of it parasitizing 22 host species (Fry *et al.* 1988). In South Africa and Zimbabwe, 58% of its records are from nests of the Cape robin *Cossypa caffra*, yet only 2.5% of nests of this host species are parasitized (Kuiper 1999). Locally, however, Cape robin parasitism rates may be higher: Oatley (1970) recorded a rate of 16% for the province of Kwazulu-Natal (South Africa), based on field observations, with 25% at one locality (Winterskloof) within that province. This discrepancy could reflect the possibility that nest record card analyses underrepresent actual rates of parasitism, as inexperienced observers do not detect mimetic cuckoo eggs. However, this is unlikely to occur in Cape robins, as cuckoo eggs usually do not appear to match eggs of this species (Rowan 1983).

Recent work by Marchetti *et al.* (1998) and Gibbs *et al.* (2000) on the common cuckoo *Cuculus canorus* has confirmed the evolution of host races (gentes), each characterized by a particular egg type which mimics, to the human eye, different host species. In the red-chested cuckoo, the most common type of cuckoo egg is uniform chocolate brown, which appears to match Heuglin's, Natal and chorister robins (Kuiper 1999). A second type is pale blue with pinkish-brown freckling, which appears to match eggs of the bearded robin (Oatley 1970), boulder chat (Steyn 1968) and the kurricane thrush (Kuiper 1999). A third type is pale brown with brown freckling, which to the human eye appears to match eggs of the black-headed weaver (Kuiper 1999). None of these gentes appears, to the human eye, to match eggs of the Cape robin (Rowan 1983), which seems to accept eggs that appear both mimetic and non-mimetic to humans (Kuiper 1999).

It is possible that hosts that accept apparently non-mimetic eggs (such as the Cape robin) do so because they lack the ability to discriminate between cuckoo eggs and their own eggs. Additionally or alternatively, there may be matching between host and cuckoo eggs, which is not apparent to the human eye. To investigate these possibilities, we compared 1100 reflectance spectra (300–700 nm) taken in a stratified, random design from clutches of red-chested cuckoo and host eggs in museum collections. Assessments of cuckoo–host matching in the same clutches by 15 independent observers who were blind to the reflectance spectra data were also performed, allowing us to determine the correlation between human assessments of similarity and the objective values of similarity derived from reflectance spectrophotometry.

2. METHODS

We studied the two most extensive egg collections of African birds—those at the British Natural History Museum and the Transvaal Museum in the province of Gauteng, South Africa—and found 21 clutches of eggs from ten species, including seven of the Cape robin, containing eggs of the red-chested cuckoo. The species composition of these clutches, together with a classification of their cuckoo egg gens and details of the number of host eggs, are listed in table 1.

For each clutch, we asked 15 human observers to record matching between each cuckoo egg and each host egg on a 1–5 scale (1 = perfect matching; 5 = no matching) using a protocol defined by Moksnes & Røskaft (1995) for the common cuckoo. For these assessments, each clutch was placed on cotton wool in a small box in a well-lit laboratory (illuminated by natural lighting plus standard fluorescent tubes), with host eggs identified by numbered spots on the cotton wool. Observers were given 15 clutches for eggs from the Transvaal Museum or six clutches of eggs from the British Natural History Museum and asked to score the degree of dissimilarity between the cuckoo egg and each host egg in the clutch. From these measures, a mean dissimilarity for each clutch was calculated. The order of presentation of clutches was randomized between observers.

Reflectance spectra 300–700 nm were obtained from all host and cuckoo eggs using a Zeiss MCS 500 spectrophotometer and Zeiss CLX xenon lamp (Carl Zeiss, Jena, Germany) measuring at 0.81 nm intervals. As in earlier studies of feathers (Bennett *et al.* 1996, 1997; Cuthill *et al.* 1999; Hunt *et al.* 1998), illumination was 45° to the surface, with reflected light collected at 135° (i.e. 90° to illumination) from a spot size *ca.* 2 mm in diameter. A stratified random sample of spectra from all regions of the eggs was obtained by dividing each egg into five regions (five bands around the long axis of the egg, each band having a width of 20% of the length of the egg). From each of these five regions, three randomly located measurements were taken. A reference calibration (from a Spectralon 99% white standard (Labsphere, Inc., North Sutton, NH, USA)) was taken prior to beginning a new region (i.e. every three spectra) and a dark current calibration prior to measuring each spectrum. Reflectance at 0.81 nm was transformed to 2.43 nm intervals by taking the mean of three adjacent measurements. The mean reflectance spectra for each egg in the clutch was calculated from the 15 spectra taken from each egg. A mean host spectrum per clutch was also calculated, as there were variable numbers of host eggs per clutch (table 1). Subsequent analyses were based on the 21 pairs of mean reflectance spectra so generated (there being 21 clutches, each with a mean host spectrum and a mean cuckoo spectrum).

Principal components analysis (PCA) was performed on these reflectance data; this reduced a large number of correlated variables (in this case reflectance at each 2.43 nm interval) into a few orthogonal variables, which summarized most of the variation (Bennett *et al.* 1997; Cuthill *et al.* 1999; Hunt *et al.* 1998; Langmore & Bennett 1999). Invariably, the first principal component (PC1) describes variation in mean reflectance, essentially brightness (sometimes also known as 'achromatic brightness'; *sensu* Endler 1990; Bennett *et al.* 1997; Cuthill *et al.* 1999; Hunt *et al.* 1998). As brightness comprises most of the variation between spectra, PC1 usually explains over 90% of the total variation in natural spectra (Hurlbert 1986; Endler & Théry 1996; Bennett *et al.* 1997; Cronin *et al.* 1997; Cuthill *et al.* 1999; Grill & Rush 2000). Principal components 2 and 3 (PC2 and PC3 respectively) represent variation in spectral shape and are therefore indirectly related to hue and saturation (Endler 1990; Endler & Théry 1996; Bennett *et al.* 1997; Cuthill *et al.* 1999; Grill & Rush 2000). Cuthill *et al.* (1999) recommend PCA analysis of reflectance spectra for studies of animal coloration for several reasons. Notable among these are that such a method objectively describes variation in reflectance, the principal components are independent of the visual system of the receiving animal and, most importantly, reflectance spectra are the invariant features of objects that we expect visual systems to have evolved to extract. Human scoring of host–cuckoo dissimilarity was compared with the principal component scores using both simple and multiple regression. As principal components are orthogonal, univariate tests on individual components are statistically independent, but a multiple regression provides a useful summary statistic for whether any aspect of reflectance spectra explains the human dissimilarity score.

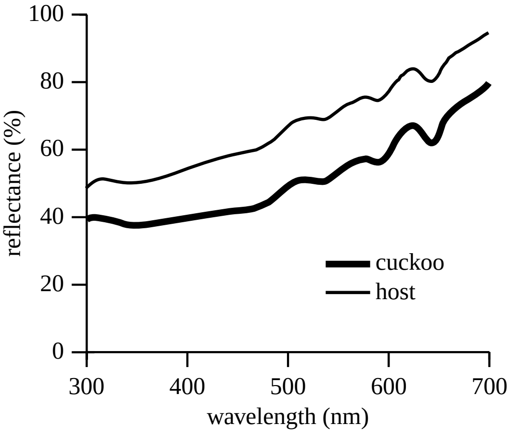

Figure 1. Mean reflectance spectra of eggs of the red-breasted cuckoo and its hosts. Host species are as shown in table 1. So that each clutch contributes equally, host values are the means of the means of each host egg within each clutch.

To determine whether the similarity observed between host and cuckoo eggs in our clutches was less than or greater than that expected due to chance alone, a Monte Carlo randomization procedure ($n = 1000$ runs) was used to generate the null expectation, in effect simulating cuckoos laying their eggs at random with respect to our sample of host nests. As above, a mean dissimilarity between cuckoo and host eggs was calculated for each randomized pairing so produced. To allow easy determination of 'matching', the standard deviation in this measure was plotted and compared with observed values, separately for scores on PC1, PC2 and PC3. A low value indicates close matching; a high value indicates mismatching.

3. RESULTS

The two mean reflectance spectra for cuckoo and host eggs are similar in general shape and are typical of a whitish-brown coloured object (see figure 1). However, the small 'ripples' between 570 and 670 nm are not a prerequisite for such colours. Similar-shaped spectra, that is with ripples in similar locations, were found when the same eggs were measured at different geometries, and when eggs of other species were measured. So while smooth reflectance spectra are common in biological objects, our results show that small undulations can also be found. This should not be a surprise as such undulations have been observed in feathers of a variety of species (e.g. Hunt *et al.* 1998; Keyser & Hill 1999), including those measured by different groups and using different spectrophotometers, and in eggs of other species (A. T. D. Bennett, unpublished results). Inspection of the mean spectra shows that host eggs reflect more at all wavelengths than cuckoo eggs, a result supported by later analyses.

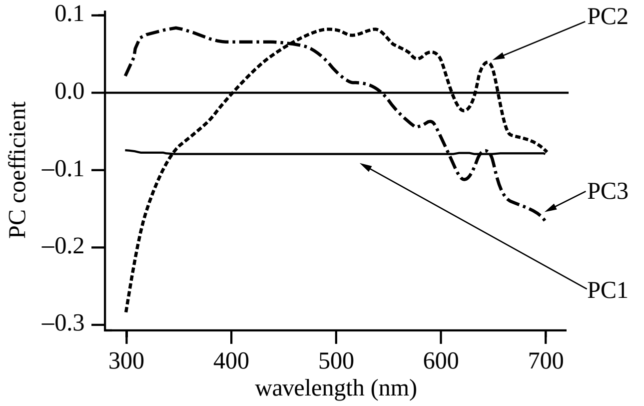

Figure 2. Principal components as a function of wavelength, derived from reflectance spectra from the cuckoo and host eggs in each clutch ($n = 42$). PC1 indicates principal component 1, PC2 indicates principal component 2 and PC3 indicates principal component 3.

Mean human dissimilarity scores for each host egg clutch are listed in table 1. Of the 21 red-chested cuckoo clutches examined in this study, six would be classified by humans as being mimetic, i.e. by having a dissimilarity score of between one and three, based on the classification system of Moksnes & Røskaft (1995). Only one (of seven) Cape robin clutches, and one (of four) kurricane thrush clutches appear mimetic to humans; the other four eggs that appear mimetic are found in the sole clutches of the black-headed weaver, and the Natal, chorister and Heuglin's robins (table 1).

The first three principal components together explain 99.8% of the variance in spectra (figure 2). PC1 explains 97.5% of the variance, is flat and consequently represents brightness (sometimes called achromatic brightness, see above). PC2 and PC3 are not spectrally flat, and so represent aspects of the eggs' chromatic (hue and saturation) variation. Together PC2 and PC3 account for 92% of the colour variance, and 2.3% of the total variance. Of the colour variance, 64% can be attributed to PC2, and 28% to PC3. PC2 is curved and high and positive at short wavelengths, and high and negative at longer wavelengths, and therefore could be described as 'the opposite of brownness'. PC3, by contrast, is curved and high and negative at UV wavelengths, and high and positive at long wavelengths, and therefore could be described as 'UV versus greenness' or some UV/greenness opponency.

The results of the random simulation (figure 3*a–c*) and paired *t*-tests indicate that within clutches, host and cuckoo eggs are marginally significantly dissimilar for their score on PC1, which represents brightness ($t_{20} = 0.418$; $p = 0.059$; figure 3*a*). That is, the cuckoo eggs are marginally significantly darker than those of their hosts. Host and cuckoo eggs are not significantly different from that predicted by the random simulation of score on PC2 ($t_{20} = 0.163$; $p = 0.479$; figure 3*b*). However, interestingly, cuckoo and host eggs are highly significantly similar for their score on PC3, which represents 'UV versus greenness' ($t_{20} = 0.671$; $p = 0.001$; figure 3*c*). That is, host and cuckoo are matched with respect to this chromatic factor.

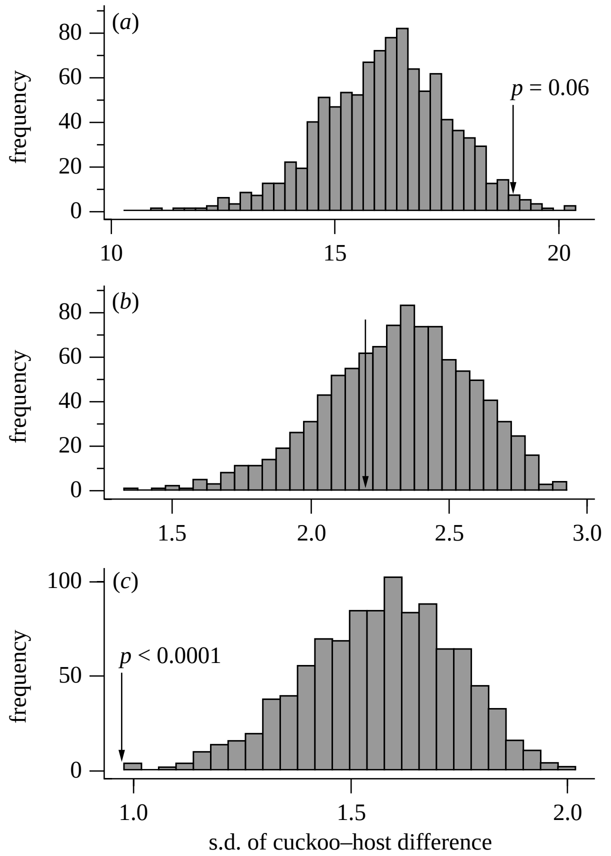

Figure 3. The expected and observed matching between host and cuckoo eggs in score on (*a*) PC1, (*b*) PC2 and (*c*) PC3. In each case, the random expectation is derived from the simulation with 1000 runs and is indicated by the frequency distribution of the standard deviation (s.d.) of differences between cuckoo and host eggs. The arrows indicate the observed degree of matching between host and cuckoo eggs on the same variable. The horizontal axis indicates the s.d. of cuckoo–host differences in scores of each principal component.

Figure 4*a–c* also relates to within-clutch variation and involves simple linear regression of absolute values of host–cuckoo differences in PS1, PS2 and PS3, against the human scoring of cuckoo–host egg dissimilarity. In this way, we can see how human assessment of egg colour matching corresponds with that derived (objectively) from principal components. PS1, which represents brightness, was not correlated with the human assessment of egg matching ($F_{1,19} = 2.64$, $p = 0.121$). However, of the three principal component scores, it was the nearest to significance. PS2, the opposite of brownness, was also not correlated with human assessment of egg matching ($F_{1,19} = 1.06$, $p = 0.315$). Finally, PS3, UV versus greenness, was not significantly correlated with the human scoring of dissimilarity ($F_{1,19} = 0.11$; $p = 0.745$). That is, host–cuckoo differences in scores on PC3, in which cuckoo and host spectra are closely matched, were also not detected by human observers ($F_{1,19} = 0.11$; $p = 0.745$).

A multiple regression using all three principal components as dependent variables did not explain a significant portion of the variation in human assessment of egg dissimilarity (r^2 (adj) = 0.123; $F_{3,17} = 1.93$; $p = 0.163$). These statistical results from regressions are robust if analyses are performed only on the 17 clutches containing the type 1 cuckoo gens, rather than on all 21 nests.

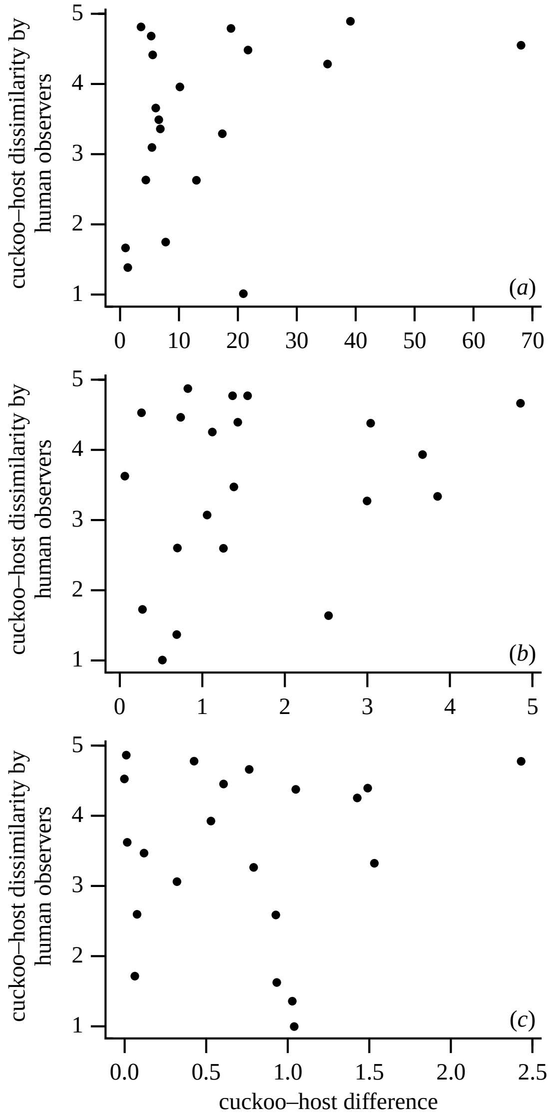

Figure 4. Cuckoo–host dissimilarity as assessed by human observers plotted against cuckoo–host difference in scores on (*a*) PC1, (*b*) PC2 and (*c*) PC3. Note that on the dissimilarity scale given by humans, a score of 1 indicates perfect matching and a score of 5 indicates maximum dissimilarity.

4. DISCUSSION

To our knowledge, this is the first study of egg coloration using reflectance spectra over the bird visible range (i.e. 300–700 nm), and several interesting features of egg mimicry not apparent to the human eye have been revealed. Notable among these are that eggs of the red-chested cuckoo and its hosts are highly matched in chromatic aspects not visible to humans, corresponding to opponency of UV and greenness. This conclusion follows from the highly significant match in PC3 between hosts and cuckoos. As this host–cuckoo matching was not detected by human observers, it indicates that humans are unable to perceive at least some host–cuckoo egg colour matching. Furthermore, there was no evidence in this study that human observers could detect any of the features in which host and cuckoos eggs matched. This has perhaps sobering implications for further attempts to assess host–cuckoo egg matching using human colour vision, or standards based thereon. Given the now ready availability of UV-visible spectrophotometric techniques for measuring colour, it would seem prudent to use such methods in the future.

Other studies on egg matching in cuckoos and egg crypsis and clutch survival (e.g. Westmoreland & Kiltie 1996) have used human colour vision (or standards based thereon) to assess egg coloration. These assessments of matching have successfully predicted host rejection behaviour in response to parasitism by the common cuckoo (Davies & Brooke 1988; Stokke *et al.* 1999). But for our data set, human assessments of dissimilarity between eggs of the red-chested cuckoo and its hosts did not correlate with brightness (PC1), brownness (PC2) or UV-greenness (PC3). PC1 accounts for 97.5% of the variance in reflectance spectra, and despite this large component, it appears that human assessments of egg mimicry do not detect differences between cuckoo and host eggs in this respect (figure 4*a*). Humans also appear unable to perceive egg matching in colour represented by PC3 ('UV versus greenness'), the component in which cuckoo and host eggs are most similar in terms of their reflectance spectra, and which accounts for *ca.* 28% of the chromatic variation.

Why are these non-mimetic eggs accepted? Previous studies have explained the enigma of why hosts often accept apparently non-mimetic eggs, either in terms of the evolutionary lag or equilibrium hypotheses. Davies *et al.* (1996) argued convincingly that below certain threshold levels of parasitism, acceptance of even apparently mimetic eggs by reed warblers can be optimal provided that rejection costs are high enough, and Brooker & Brooker (1996) have similarly argued that the cost of acceptance of cuckoo eggs by splendid fairy-wrens can be low enough in terms of lifetime reproductive success to be an evolutionarily stable strategy. Both of these arguments may apply to the red-chested cuckoo system as well because all of the ten host species measured in this study (six of which are 'non-mimetic') have been recorded in the literature as feeding nestling or fledgling red-chested cuckoos (Rowan 1983), indicating that these host species must accept cuckoo eggs to some extent at least.

However, another possible explanation for our results and for the acceptance of 'mimetic' and 'non-mimetic' eggs of the red-chested cuckoo by the Cape robin (Kuiper 1999) is that host–cuckoo egg discrimination is performed only with certain combinations of wavelengths. In this way, cuckoo eggs that appear non-mimetic to humans could be perceived as a good match by their avian hosts. This could arise by one or more of the following mechanisms. First, 'hardwiring' of the avian visual system could mean that only certain wavelengths in the 300–700 nm range are used in egg discrimination. However, as birds are probably tetrachromatic (Bennett *et al.* 1996; Bowmaker *et al.* 1997), it is unlikely that certain wavebands are excluded altogether. Nevertheless, there are too few studies at this stage to rule out such possibilities, and examples of fivefold differences in spectral sensitivities over the bird visible range, as reported for a passerine by Burkhardt & Maier (1989), suggest that unequal contributions of different cone types to avian colour vision may exist. The fact that the southern olive thrush *Turdus* *olivaceus*, in contrast to the Cape robin, can distinguish between 'mimetic' and 'non-mimetic' eggs (Kuiper 1999) could reflect differences in spectral sensitivity between the two species that may or not be related to past selection pressures. Further experimental work on matching (using spectrophotometric measurements) and rejection behaviour is clearly warranted.

A second possible mechanism leading to acceptance of non-mimetic cuckoo eggs involves the different light environments likely to be found in nests of these and other host species. While large variation in light environments of different habitats (Endler 1993) have been argued to influence the evolution of colour patterns of guppies (Endler 1978) and birds (Endler 1993; Endler & Théry 1996), the role of light environments in the evolution of egg coloration has not yet been investigated. We simply extend the light environment hypothesis and suggest that light environments may hinder egg discrimination by cuckoo hosts, and thus under some circumstances could lead to the acceptance of non-mimetic eggs.

A third plausible mechanism leading to our results, and the enigmatic apparent acceptance of mimetic and non-mimetic eggs, is spatial autocorrelation in the diet of hosts and cuckoos. In this way, eggs of cuckoos and hosts in the same locality could have similar coloration, not as a consequence of selection for matching, but rather as a consequence of similar diets or other similarities in factors in the local environment which could influence egg colour. Museum specimens are obviously drawn from a wider range of localities, so this hypothesis predicts that host and cuckoo eggs from the same nest tend to be more alike than the simulated random pairings of host and cuckoo eggs. This was exactly the result we found.

Finally, our study raises the intriguing question of what exactly is meant by the commonly used term 'egg matching' in studies of cuckoos. Does it mean matching: (i) as perceived by humans; (ii) as indicated by spectrophotometric measurements over the bird visible range; (iii) as perceived by brood parasites themselves; or (iv) as perceived by hosts? Only experimental studies could resolve differences in the last two categories, as visual perception may well differ between cuckoos and their mainly passerine hosts, Bowmaker *et al.* (1997) and Vorobyev *et al.* (1998) having documented differences in oil droplets, visual pigments and spectral sensitivity in different classes of birds. Hitherto, studies have not distinguished between these different definitions of egg matching, and future work could usefully focus on these aspects.

In summary, our study reveals aspects of cuckoo–host egg matching that are not noticed using human vision. If such phenomena are general, there are subtleties and complexities in the evolution of host–cuckoo egg mimicry that were not previously suspected. These may help to explain the paradox that some host species accept eggs that appear to humans to be non-mimetic. Avian and human colour vision differs in several ways, and these differences are used in a variety of tasks, including mate choice and foraging. Results here suggest that one should not be surprised if such differences are also used in discrimination of eggs of brood parasites.

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