



## Rejection of parasitic eggs in relation to egg appearance in magpies

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The coevolutionary process between avian brood parasites and their hosts predicts that low intraclutch variation in egg colour appearance favours egg discrimination of parasite eggs by hosts. Low intraclutch variation would also result in high interclutch variation, which would increase the difficulty of evolution of mimicry by the cuckoo, because many host colour patterns might coexist in the same host population. We explored this possibility using an experimental approach in the common magpie, *Pica pica*, and great spotted cuckoo, *Clamator glandarius*, system. We artificially parasitized magpie nests with great spotted cuckoo model eggs to assess host response in two populations in Spain (Guadix and Doñana) in relation to intraclutch variation in egg appearance, measured by ultraviolet–visible reflectance spectrophotometry. Individuals that rejected model cuckoo eggs had higher intraclutch variation than accepters, suggesting that an increase, rather than a decrease, in intraclutch variation in magpie egg appearance was advantageous for cuckoo egg discrimination.

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Egg colour in birds is highly variable between and within species. Several functional explanations have been proposed to explain such extreme variability in egg colour (reviewed in Underwood & Sealy 2002). For example, eggs of species that are laid directly on the ground are much more cryptic than others because they are under a higher risk of predation (Tinbergen et al. 1962; Solís & de Lope 1995). However, in species where parents build a nest cup, predators find nests mainly by monitoring nest-building activity of parents or by searching for nests, making egg crypsis of secondary importance and making nest conspicuousness the trait under selection (Götmark 1992). A second functional explanation of egg colour patterns is related to the identification of own eggs by parents in high-density colonies (Birkhead 1978). However, evidence precludes individual clutch recognition, because Caspian terns, *Sterna caspia*, common guillemots, *Uria aalge*, and

thick-billed murre, *U. lomvia*, nesting in dense colonies still found their nest sites when both clutches and nests were removed (Tschanz 1959; Shugart 1987; Gaston et al. 1993).

A third functional explanation of egg coloration in birds is related to brood parasitism, a reproductive strategy in which certain individuals (parasites) receive parental care from unrelated individuals (hosts). Parasitized hosts usually suffer reduced reproductive output (Røskoft et al. 1990; Payne 1997). Parasitism thereby favours the evolution of host defences, which simultaneously select for more sophisticated trickeries by the parasite to overcome host defences (Davies & Brooke 1988). This coevolutionary ‘arms race’ leads to intricate adaptations and counter-adaptations by both sides, where each party responds to the selective forces imposed by the other (Dawkins & Krebs 1979; Soler & Møller 1990). A generalized host defence against brood parasites is the recognition and rejection of parasite eggs from their nests, which selects for egg mimicry by cuckoos. Thus, coevolution between hosts and parasites improves egg mimicry by the cuckoo and egg discrimination by the host (Davies & Brooke 1988; Soler & Møller 1990).

The arms race hypothesis assumes that one step in the coevolutionary interaction between cuckoos and their hosts is a reduction in intraclutch variation in egg

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appearance of hosts. This reduced variation would facilitate discrimination of parasite eggs from own eggs when cuckoo egg mimicry is very accurate (Victoria 1972; Davies & Brooke 1989b). Furthermore, increasing variation in phenotype between clutches (i.e. interclutch variation) would be adaptive because cuckoo eggs should mimic the most frequent egg colour and pattern in the host population (Soler & Møller 1996), so individuals with more extreme phenotypes would more easily recognize foreign eggs. Most evidence concerning the relation between intraclutch variation of hosts and egg recognition derives from comparative analyses. These analyses show that passerine species commonly parasitized by the cuckoo have evolved lower intraclutch variation in egg appearance, and higher interclutch variation than those that have not been parasitized (Øien et al. 1995; Soler & Møller 1996; Stokke et al. 2002). Furthermore, intraspecific evidence also suggests that a reduction of intraclutch variation is a stage in the coevolutionary arms race between host and parasite, because rejecter individuals have less intraclutch variation in egg appearance than do acceptor individuals (Stokke et al. 1999; Soler et al. 2000).

In this study, we estimated intraclutch variation in egg appearance in common magpies, *Pica pica*, using spectrophotometry over the 300–700 nm range of vision. In Europe this species is the main host of the great spotted cuckoo, *Clamator glandarius*, and we explored the importance of such variation for host discrimination against parasite eggs. We studied two breeding populations that are regularly parasitized by the great spotted cuckoo. According to the arms race hypothesis, we predicted that individuals able to recognize and reject cuckoo model eggs would have lower intraclutch variation than acceptor individuals.

## METHODS

### Study Areas

The field study was carried out in southern Spain in the Hoya de Guadix near Granada (37°18'N, 3°11'W) during April–May 2001, and in Doñana National Park (37°44'N, 3°28'W) during April 2001. The Hoya de Guadix is in a high-altitude plateau, approximately 1000 m above sea level. Doñana National Park is a low-altitude high-density area where the magpie population has suffered from great spotted cuckoo parasitism since at least 103 years ago (Baker Catalogue, Natural History Museum, Section Ornithology, Tring, Herts, U.K.).

### The Study Species

The magpie is a monogamous passerine typically used as a host by the brood-parasitic great spotted cuckoo in this region. The current prevalence of great spotted cuckoo parasitism in the study magpie populations is 54.8% in the Hoya de Guadix ( $N = 431$  nests from 1982 to 1994; Soler et al. 1998) and 7.4% in Doñana ( $N = 27$ , present study). Magpies in southern Spain usually lay six or seven eggs (range 2–10; Soler et al. 1996). Only females

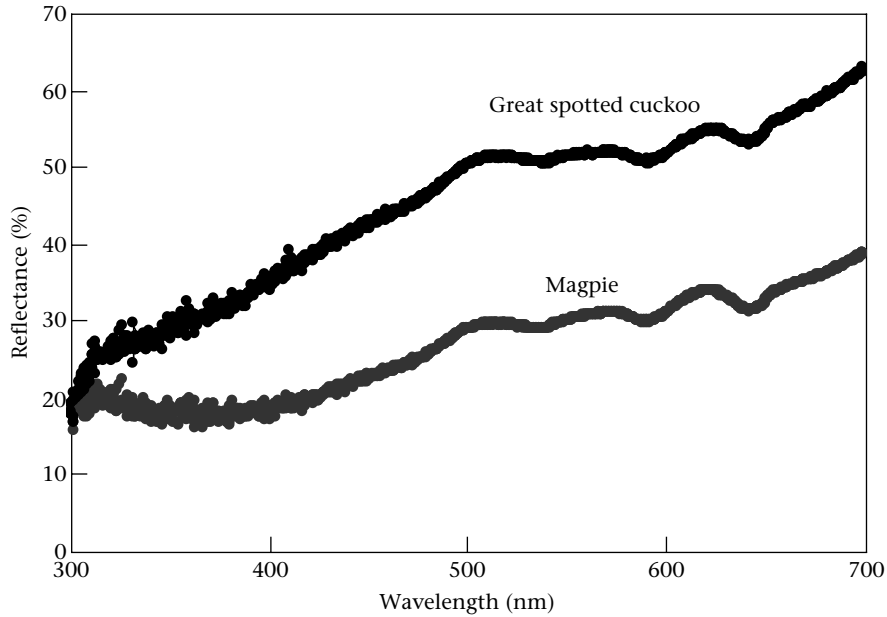
incubate the egg, starting some days after the first egg is laid (Birkhead 1991).

To the human eye, the eggs of the great spotted cuckoo appear to mimic those of the magpie (Alvarez et al. 1976). However, spectrophotometric analyses have revealed differences between the spectral characteristics of the eggs of these two species (Soler et al. 2003). The mean reflectance spectra for the magpie and great spotted cuckoo eggs that we sampled had similar general shapes and were typical of whitish-green coloured objects (Fig. 1). The mean spectra show that great spotted cuckoo eggs reflect more at all wavelengths than do host eggs (Soler et al. 2003). The magpie is able to discriminate against foreign eggs and eject them from its nest depending upon the level of mimicry of these eggs (Soler & Møller 1990). Great spotted cuckoo parasitism lowers magpie breeding success (Soler et al. 1996), providing the basis for a coevolutionary arms race between magpie defences and parasite counter-defences (Soler & Soler 2000).

### Data Collection

At the beginning of the breeding season, we searched for magpie nests. We found 27 nests in Doñana before egg laying began, and 36 nests from the Guadix population; four of these were found after clutch completion but with no sign of parasitism, i.e. there were no crushed eggs, and clutch size was similar to that of nonparasitized nests. We mapped all nests, visited them daily and numbered each egg with waterproof ink in consecutive order as it was laid. We detected no cases of intraspecific parasitism, because only one egg ever appeared on a single day.

To identify the discrimination abilities of individuals, we introduced one great spotted cuckoo model egg into all monitored nests. Model eggs had approximately the same size and mass as real cuckoo eggs, and they were made of plaster of Paris and painted with acrylic paint to mimic the colour and spotted pattern of real cuckoo eggs in the area (Soler & Soler 2000). However, the artificial models differed in their mean reflectance spectra from the magpie and the great spotted cuckoo eggs both in the ultraviolet (UV; 300–400 nm) and the human-visible (400–700 nm) regions of the spectra (J. M. Avilés, J. J. Soler, M. Soler & A. P. Møller, unpublished data). Therefore, magpies perceived the model eggs as nonmimetic cuckoo eggs. Earlier experimental eggs were added to magpie nests at the six-eggs stage; thus, in all experimental nests, hosts were able to assess intraclutch variation of the entire clutch, for which we collected spectroradiometric measures. In no case did artificial parasitism cause hosts to remove their own eggs on subsequent days. We considered the model egg to be accepted if it remained in the nest 2 days after artificial parasitism and as rejected when the model was absent or when the magpie nest was deserted. We have used a 72-h period to study magpie rejection behaviour (Soler & Møller 1990; Soler et al. 1999). However, magpie rejection of experimental eggs occurs mainly within 24 h from artificial parasitism; we have found that 75% of all rejected experimental eggs at 72 h occurred in the first



**Figure 1.** Examples of reflectance spectra of magpie ( $N = 14$ ) and great spotted cuckoo ( $N = 12$ ) eggs. Values are mean reflectance values at each 0.36 nm obtained from eggs belonging to four parasitized clutches at Doñana. Each clutch contributes equally, because values are the means of the means of each host and parasite egg within each clutch.

24 h (J. M. Avilés, J. J. Soler, M. Soler & A. P. Møller, unpublished data).

### Estimation of Intraclutch Variation

The estimation of intraclutch variation in egg appearance has been based on human assessment of egg similarity using an arbitrary scale (Lotem et al. 1995; Øien et al. 1995; Stokke et al. 1999, 2002). Approaches based on human vision have two main problems. First, human observers cannot perceive UV (300–400 nm) information that birds can detect because one cone in the avian retina is sensitive to UV light (Bowmaker et al. 1997). Second, the assessment of intraclutch variation based on human vision might be insufficiently sensitive to variation in colour components that birds might be able to detect, even within the human-visible range (400–700 nm), because of anatomical differences between avian and human eyes (Cuthill et al. 2000). Studies based on spectrophotometry have confirmed discrepancies between human and bird assessment of colour, because the eggs of the red-chested cuckoo, *Cuculus solitarius*, and its African hosts are highly matched for chromatic aspects of eggs invisible to humans (Cherry & Bennett 2001).

To avoid these biases, we objectively assessed egg appearance by using spectrophotometric techniques in the field. Reflectance spectra in the 300–700-nm range were obtained from all eggs of the 36 analysed clutches in Guadix and from all eggs of 12 clutches in Doñana using a spectroradiometer (Ocean Optics Europe, Eerbeek, The Netherlands). We did not measure egg colour appearance in 15 clutches in Doñana in which we tested rejection behaviour because of logistic problems with colour

equipment during data collection. These problems were not linked to any specific area or time during data collection, so we assume that egg appearance values from the 12 clutches are representative for the population in Doñana in 2001.

Colour was always measured twice in two randomly selected areas of the surface of the eggs, each circa  $1 \text{ mm}^2$ . The illuminant was a deuterium and a halogen light source (DH 2000 model, Eerbeek, The Netherlands). The light was transferred to the eggs through a quartz optic fibre and reached the eggs at a  $45^\circ$  angle. The sampling optic was placed at  $45^\circ$  to the surface of the sample in the same plane of incidence as the light source fibre and was connected to a spectrometer (S2000) by a second quartz fibre optic cable. Data from the spectroradiometer were converted into digital information by DAQ Card 700 and passed into a computer with appropriate software (Spectrawin 4.1, Top Sensor System, Eerbeek, The Netherlands). The measurements were relative and referred to a standard white reference (WS-2) and to the dark. A reference and dark calibration were made before the beginning of measurement of each clutch. Total reflectance was obtained for the UV (300–400 nm), blue (400–475 nm), green (475–550 nm), yellow (550–625 nm) and red (625–700 nm) intervals. We estimated mean reflectance in these intervals by dividing total reflectance in each interval by its amplitude (nm).

Spectrophotometric techniques may have some limitations for reporting global egg appearance in a spotted egg. When speckles are large, it is necessary to provide spectral measures for both the spots and the background egg colour. When speckles are small, the spectral measurements are weighted averages of the spots and the background egg colour, and this can affect egg colour

assessment. For instance, with a single spectrophotometric measure per egg, it may be difficult to distinguish between colour from spots and that from the background of the egg. It is also not possible to distinguish between different patterns of spottiness, which could be important for birds distinguishing between their own and foreign eggs. However, repeatability analyses of different measures from randomly selected areas allow us to determine colour variability within individual eggs (Falconer & Mackay 1996). When repeatability does not reach statistical significance because of nonrandom distribution of spots within the egg, measures on different parts of the eggs with different spot patterns should be performed and analysed separately. Magpie eggs are finely speckled and show a random distribution of spots in their eggs. Thus, we used two measures of the repeatability of our estimate of reflectance. First, we measured twice in the same randomly selected area of a single egg and found a high repeatability for all variables (repeatability  $> 0.94$ ,  $P < 0.0001$ ). Second, we measured each egg in two randomly selected areas and found a significant repeatability (repeatability  $> 0.77$ ,  $P < 0.001$ ). Thus, all our measurements were reliable, so we used mean values for each egg for each established interval.

We computed objective reflectance parameters relevant to an avian perceptual colour space from these total reflectance values. Total intensity of light reaching the avian eye from the egg (brightness; Endler 1990) was the sum of total reflectance values for UV and visible wavelength intervals ( $R_{300-700}$ ). We used reflectance ratios ( $R_{300-400}/R_{300-700}$ ;  $R_{400-475}/R_{300-700}$ ;  $R_{475-550}/R_{300-700}$ ;  $R_{550-625}/R_{300-700}$  and  $R_{625-700}/R_{300-700}$ ) as estimations of 'UV chroma', 'blue chroma', 'green chroma', 'yellow chroma' and 'red chroma', respectively. To estimate the degree of intraclutch variation, we calculated the standard deviation of brightness, UV chroma, blue chroma, green chroma, yellow chroma and red chroma in a magpie clutch. This is the most reasonable way of measuring variation in egg appearance in a clutch, because microspectrophotometric studies of the visual pigments of the magpie are lacking, and therefore sensitivities at different wavelengths cannot be estimated. Furthermore, information from microspectrophotometry exists for only seven passerines (Cuthill et al. 2000). The rook, *Corvus frugilevus*, is the species most closely related to the magpie for which such information is available, and in this species, only the location of the spectral cones at medium and large wavelengths has been determined. Therefore, we considered it prudent to make no assumptions about specific sensitivity in magpies.

Studies have advocated the use of Principal Component Analyses (PCA) for describing reflectance spectra (Cuthill et al. 1999; Cherry & Bennett 2001). The aim of our study was not to define differences in spectral reflectance or shape but to obtain a reliable measure of variation in reflectance within a clutch. Using PCA for our purposes would imply calculating a measure of variation on scores from the PCA within each clutch that might have not a simple biological interpretation. Furthermore, the scores of a PCA are weighted averages of the spectral measures at all the wavelengths, so PCA is presumably a less powerful

approach for detecting differences arising in only some regions of the spectrum. Therefore, we considered it more appropriate for the purposes of this study to estimate intraclutch variation at the five arbitrarily chosen wavebands.

## Statistical Analyses

Intraclutch variation in all colour variables in both Guadix and Doñana fitted normality assumptions (Kolmogorov–Smirnov tests for continuous variables;  $P > 0.2$  in all cases; Zar 1996). Partial correlations were used to analyse the association between laying date and each of the six colour variables while controlling for the other colour variables. We used logistic regression to study the association between rejection behaviour of model eggs and laying date of the magpie.

Because colour variables are typically related (Endler 1990), we tested for changes in magpie defences to great spotted cuckoo parasitism using MANCOVA models with the six intraclutch colour components as dependent variables, clutch size as a covariate and response to artificial parasitism (rejecter versus acceptor) as a factor. When the MANCOVA yielded a significant result, we proceeded to individual ANCOVAs (Scheiner 2001). Throughout, when using two or more tests for testing a common null hypothesis, we applied sequential Bonferroni correction for the probability of a type I error (Rice 1989).

## Ethical Note

Our hypothesis required the inclusion of model eggs in experimental magpie nests. As far as we could determine, no magpie eggs were crushed as a result of our manipulations, and we detected no effect on magpie egg hatching relative to nonexperimentally treated nests. Our study was carried out under special licences from the Spanish government and Junta de Andalucía for animal experiments.

## RESULTS

In Guadix, great spotted cuckoo model eggs were rejected from 15 (41.7%) of 36 magpie nests. Intraclutch variation in egg appearance differed between acceptor and rejecter magpies (Wilk's  $\lambda_{6,28} = 0.64$ ,  $P = 0.04$ ), with rejecters showing higher variation in green chroma than acceptors (Table 1). The probability of magpies rejecting model eggs was not significantly associated with laying date in Guadix (acceptors:  $\bar{X} \pm \text{SD} = 16.89 \pm 4.06$ ,  $N = 19$ ; rejecters:  $15.84 \pm 5.09$ ,  $N = 13$ ; chi-square test:  $\chi^2_1 = 0.44$ ,  $P = 0.68$ ). Furthermore, we detected no seasonal pattern of intraclutch variation because none of the variables was significantly associated with laying date (Table 2). Mean clutch size of rejecter and acceptor pairs did not differ significantly (rejecter:  $\bar{X} \pm \text{SD} = 6.61 \pm 0.97$ ,  $N = 21$ ; acceptor:  $7.13 \pm 0.91$ ,  $N = 15$ ; ANOVA:  $F_{1,34} = 2.56$ ,  $P = 0.12$ ).

**Table 1.** Mean ± SD intraclutch variation in egg colour of magpie eggs in relation to rejection behaviour towards model cuckoo eggs

	Accepters of model cuckoo egg (N=21 clutches)	Rejecters of model cuckoo egg (N=15 clutches)	F <sub>1,33</sub>	Mean square	P
Brightness	933.60±545.9	1039.59±365.03	0.15	231 095.14	0.70
Chroma					
UV	0.95±0.37	0.79±0.22	3.11	0.10	0.08
Blue	0.69±0.30	0.79±0.20	0.58	0.07	0.45
Green	0.58±0.21	0.78±0.25	7.65	0.05	0.009*
Yellow	0.57±0.28	0.53±0.26	1.15	0.06	0.29
Red	1.10±0.52	1.29±0.55	0.21	0.25	0.64

The last three columns show individual ANCOVA results. \*P < 0.05 after Bonferroni correction.

In Doñana, great spotted cuckoo model eggs were rejected from 13 (54.2%) of 24 nests, not differing significantly from that reported for Guadix (Fisher’s exact test: P = 0.43). Intraclutch variation in egg appearance did not differ significantly between Doñana and Guadix (Wilk’s lambda<sub>6,40</sub> = 0.77, P = 0.08; Table 3). The small sample size in Doñana precluded multivariate analyses of egg appearance in relation to magpie rejection behaviour. However, rejecter magpies had higher intraclutch variation in green chroma than accepters (accepters:  $\bar{X} \pm SD = 0.69 \pm 0.65$ , N = 7; rejecters:  $1.31 \pm 0.23$ , N = 4, F<sub>1,9</sub> = 5.29, P = 0.046).

**DISCUSSION**

Egg discrimination is a widely used defence tactic by hosts against brood parasitism (Davies & Brooke 1989a; Rothstein 1990), indicating reciprocal selective influences between the parasite and its hosts (Davies & Brooke 1989b; Moksnes et al. 1990). Two major mechanisms acting at two levels have been proposed to favour the recognition of parasite eggs. First, the reduction in intraclutch variation of host eggs allows the host to discriminate parasite from own eggs (Victoria 1972) more effectively. Second, high interclutch variation in egg appearance increases the difficulty of evolution of mimicry by the cuckoo, because many host colour patterns might coexist in the same host population (Victoria 1972; Davies & Brooke 1989b). Egg colour and spottiness are genetically determined in birds, with one female laying

similar eggs throughout life (Victoria 1972; Collias 1993), so the study of intraclutch variation as the mechanism favouring egg discrimination precludes biases from flexible host responses to parasitism (e.g. Davies et al. 1996).

In the present study, we tested the first of these mechanisms using objective techniques of colour assessment of magpie eggs. When we statistically controlled for clutch size, acceptor individuals showed lower intraclutch variation in green chroma than did rejecter individuals. The importance of green chroma in explaining the magpie rejection behaviour in Guadix and that the same colour feature also explained rejection in Doñana are difficult results to explain by chance. We measured six variables, and the probability of finding the same result, assuming that at least one would significantly explain our dependent variable, is very low (P = 0.028). Therefore, our results suggest that great spotted cuckoos select for higher intraclutch variation in green chroma in magpie eggs.

The mechanism underlying the importance to magpies of green but not of other colour components to discriminate parasitic eggs is unknown, but it may be related to the observation that parasitic eggs are nonmimetic in brightness to those of magpies (Fig. 1). Researchers have claimed that great spotted cuckoo eggs are a perfect example of complete evolution of mimicry (Jourdain 1925; Baker 1942). However, we suggest that great spotted cuckoo egg coloration and patterns are not the result of the coevolutionary process with their hosts, but instead are apomorphic traits (i.e. derived or advanced features that arose relatively late in members of a group), because

**Table 2.** Partial correlations between laying date and intraclutch colour variation in the magpie in Guadix

	r	r <sup>2</sup>	t <sub>24</sub>	P
Brightness	-0.22	0.79	-1.15	0.25
Chroma				
UV	0.06	0.53	0.33	0.73
Blue	0.04	0.69	0.20	0.83
Green	-0.02	0.23	-0.13	0.89
Yellow	0.05	0.69	0.26	0.79
Red	0.09	0.63	0.51	0.61

**Table 3.** Mean ± SD intraclutch variation in egg colour of magpie eggs in Guadix and Doñana

	Guadix (N=36 clutches)	Doñana (N=12 clutches)
Brightness	977.75±475.81	922.81±342.21
Chroma		
UV	0.88±0.33	1.08±0.42
Blue	0.73±0.26	0.86±0.51
Green	0.67±0.24	0.88±0.50
Yellow	0.56±0.27	0.71±0.27
Red	1.18±0.54	1.43±1.04

changes in the appearance of great spotted cuckoo eggs do not parallel those of their hosts (Soler et al. 2003). Furthermore, the largest differences between great spotted cuckoo and magpie eggs were in the green chroma (Soler et al. 2003), which implies that the related reflectance would be an important trait to help magpies to distinguish between parasitic and own eggs. Lower intraclutch variation should become more important as mimicry improves. However, the appearance of the parasitic egg differs from that of its main host in Europe (Soler et al. 2003). Thus, magpies should be able to discriminate parasitic eggs even if their own eggs are highly variable. However, even assuming imperfect evolution of mimicry in the system, it is difficult to imagine a situation in which greater egg variability would directly facilitate foreign egg recognition, and a genetic correlation with that ability is then a probable explanation.

Another possible explanation of our results is that older magpies have more intraclutch variation in green chroma because the production of egg pigmentation may change with age (Solomon 1991). Egg discrimination by hosts is probably based on a learning mechanism (Victoria 1972; Lotem et al. 1992), so the detected pattern should be a consequence of the greater recognition abilities of parasitic eggs by older magpies and not egg appearance. This hypothesis predicts that great spotted cuckoos should prefer young magpies as hosts because they have poorer recognition abilities. We cannot test this possibility, because it is not known how the decline in pigment production with age may affect egg appearance within a clutch. Furthermore, the magpies in the present study were unmarked. However, this explanation seems unlikely, at least for this system, because great spotted cuckoos select magpie hosts in relation to parental quality (Soler et al. 1995), which is positively related to age.

Alternative explanations for our results could be related to other selective pressures acting on egg appearance of birds. Two major forces influencing egg appearance besides interspecific brood parasitism are intraspecific brood parasitism and nest predation (reviewed in Underwood & Sealy 2002). Intraspecific brood parasitism is a widely used breeding strategy among colonially breeding birds (Brown & Brown 1988, 1989; Yom-Tov 2001) and species with precocial young (Andersson 1984; Yom-Tov 2001). Victoria (1972) predicted that, just as in species that are affected by interspecific brood parasitism, lower intraclutch variability and higher interclutch variability might increase the chance of discrimination of conspecific eggs when the probability of intraspecific brood parasitism is high. Møller & Petrie (1991), using 15 closely related pairs of less and more socially breeding bird species, found support for the first prediction, that lower intraclutch variability increases egg discrimination, because less social species had larger intraclutch variability in egg appearance than more social ones. However, their analyses did not support the prediction regarding interclutch variation. Yom-Tov (2001) included the magpie as one of the 13 Western Palaearctic passerine species suffering from intraspecific brood parasitism based on sporadic evidence that eggs had been moved between nests in a North American population (Trost & Webb 1986). However, in

long-term studies of magpies in the U.K. (Birkhead 1991) and Spain (this study) in which eggs were numbered, there was no evidence of intraspecific brood parasitism. Similarly, studies of magpie parentage revealed no evidence of intraspecific brood parasitism (Parrot 1995). This result implies that interspecific brood parasitism should be a more important selective pressure on magpie egg phenotype than intraspecific brood parasitism.

Nest predation is an important factor explaining the adaptive significance of egg coloration in birds that lay their eggs on the ground (reviewed in Underwood & Sealy 2002). However, changes in egg coloration explained changes in egg predation in only 10% of the studies where eggs were artificially placed in nests (Underwood & Sealy 2002). Furthermore, Götmark (1992) found evidence suggesting that predators find nests rather than eggs, which would remove any selective advantage to them for particularly coloured eggs in conspicuous nests. Magpie nests are large, distinctive and durable, constituting a good example of conspicuous nests (Birkhead 1991). Furthermore, 80% of magpie nests in Europe are domed (Birkhead 1991), suggesting that nest predation is a minor factor influencing changes in variability in egg colour.

Thus, we conclude that the most likely explanation for our results is that magpie egg coloration is affected by interspecific brood parasitism by the great spotted cuckoo. We draw this conclusion mainly because variation in egg appearance was consistently linked to a higher ability to recognize parasite eggs in current host populations.

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