Host recognition of parasite eggs and the physical appearance of host eggs: the Magpie and its brood parasite the Great Spotted Cuckoo

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Abstract. The evolution of mimicry by avian brood parasites and egg recognition by hosts is one of the most clear examples of coevolution in nature (Rothstein, 1990). Several mechanisms of host recognition have been proposed. The learning by the host to identify its own eggs is generally accepted as a first step in discriminating between its own and foreign eggs, and it has been proposed that a reduction in host intra-clutch variation would facilitate the learning process in the host. Using a computer-image analysis program, we show that ejection of non-mimetic model eggs by Black-billed Magpies (*Pica pica)* can be explained only by magpie clutch characteristics, particularly a low degree of intra-clutch variation, while the difference between mean color value of model eggs and the Magpie clutch is responsible for ejection of mimetic models. Host ejection based on differences between the parasitic Cuckoo and host eggs acts as a selective force in the evolution of mimetic Cuckoo eggs. As predicted, a reduced intra-clutch variation in the Magpie leads to large differences between the Cuckoo egg and those of the host. This relationship may be even more important in magpie hosts parasitized by the Great Spotted Cuckoo (*Clamator glandarius*), which does not apparently modify the appearance of its eggs.

Key words: Arms race, brood parasitism, *Clamator glandarius*, coevolution, egg mimicry, host egg recognition, *Pica pica*.

Resumen. *Reconocimiento de los huevos parásitos por parte del huésped y la apariencia de los huervos parásitos: la urraca y su parásito de cría el cuco.* La evolución del mimetismo de huevos por parte del parásito de cría y de reconocimiento de huevos extraños en sus nidos por parte de los hospedadores es uno de los ejemplos más claros de coevolución en la naturaleza (Rothstein 1990). Para el reconocimiento de huevos por parte del hospedador han sido propuestos varios mecanismos. Generalmente se acepta que un primer paso para reconocer huevos extraños sería que el hospedador debe de aprender a reconocer sus propios huevos. Una reducción en la variación de los huevos de una puesta facilitaría este aprendizaje y, además, disminuiría los riesgos de confundir sus huevos con otros de un parásito de cría. En este artículo, estudiamos esta hipótesis con un experimento de reconocimiento de huevos y usando un programa de ordenador para analizar imágenes. Mostramos que la expulsión de huevos experimentales no miméticos por parte de las Urracas (*Pica pica*) esta relacionado con características intrínsecas de la puesta (baja variación intra-puesta). Por otra parte, las diferencias entre el valor medio del color del modelo experimental y el de la puesta de las urracas explican la expulsión de modelos miméticos. La expulsión de huevos basada en diferencias entre los huevos del parásito de cría y los del hospedador actúa como una fuerza selectiva en la evolución del mimetismo de los huevos del parásito. De acuerdo con la hipótesis de trabajo, una variación intra-puesta reducida en las puestas de urraca lleva consigo unas mayores diferencias entre los huevos de urraca y de críalo (*Clamator glandarius*), una especie en la que aparentemente no modifica el aspecto de sus huevos con relación al hospedador que parasita.

Introduction

Avian brood parasitism is a reproductive strategy by which the parasitic species lays its eggs in the nests of other species (hosts), which incubate the eggs and rear the parasite nestlings. Brood parasites strongly reduce the reproductive success of their hosts (Rothstein, 1990), and intense parasite pressure can reduce the host population to the point of extinction (May and Robinson, 1985). However, if some individuals in the host population evolve counter-defenses against the parasites, depending on the rate of parasitism that the host population is suffering, such traits will quickly be favored by natural selection because they reduce the risk of parasitism. Egg discrimination is one of the most important defense tactics used by hosts which may lead to parasitic counter-defenses such as egg mimicry (Davies and Brooke, 1988; Rothstein, 1990), indicating reciprocal selective influences between the parasite and its hosts (Davies and Brooke, 1989b; Moksnes et al., 1990). In this scenario Øien et al. (1995) described different stages in the coevolutionary arms race between the European Cuckoo (*Cuculus canorus*) and its hosts. At first, the hosts showed no rejection behavior, accepting even non-mimetic eggs. When egg recognition emerges, selection favors rejection of non-mimetic eggs by the host, and, subsequently, due to this rejection behavior, mimetic eggs are favored in the parasite population. At this point, both host and parasite become engaged in an evolutionary arms race, fine tuning host recognition and parasite egg mimicry. There are several possible outcomes of this race: (i) extinction of the host population if the parasite egg mimicry outstrips the recognition ability of the host; (ii) the parasite can switch to a new host species if egg recognition by the host overwhelms parasite mimicry; or (iii) due to constraints on egg discrimination by the host, an equilibrium can be reached between host recognition and parasite-egg mimicry (Lotem et al. 1995). This equilibrium can be upset by ecological changes that affect the costs and/or benefits of egg rejection by the host and, therefore, it could intensify the selection pressure on the parasite to increase mimicry or change to another host.

In a comparative study, Øien et al. (1995) described variation in egg color and marking patterns in European passerines in relation to parasitism by the European Cuckoo. However, they did not control for common phylogenetic ancestry and the conclusions were not decisive. We re-analyzed these and additional data for European passerines, taking into account the phylogenetic relationships between the different passerine species and found that the evolution of egg patterns in hosts is associated with different stages of coevolution with the brood parasite (Soler and Møller, 1996). In agreement with the predictions of the arms-race hypothesis on variation of host eggs in relation to the stage of host-parasite coevolution (see Øien et al., 1995 for further information), suggesting that brood parasitism would select for a reduction in host intra-clutch variation (Victoria, 1972; Freeman, 1988; Davies and Brooke, 1989a; Møller and Petrie, 1991; Øien et al., 1995), we found that species with a lower intra-clutch variation had high rejection rate of non-mimetic eggs. As an evol-utionary consequence, these species showed a high degree of inter-clutch variation compared to those with a low level of foreign egg recognition (Soler and Møller, 1996).

In the present paper, we study the possible relationship between the behavioral response of acceptance or ejection of foreign eggs by the host, and the host genetic response of laying a clutch with low variation. We have studied the Black-billed Magpie (*Pica pica*), which is the main host of the Great Spotted Cuckoo (*Clamator glandarius*) in Europe. In this parasite-host relationship, the eggs of the Great Spotted Cuckoo appear to mimic those of the Magpie host (Alvarez et al., 1976), while the Magpie is able to recognize foreign eggs and eject them from the nest (Alvarez et al., 1976; Soler, 1990; Soler and Møller, 1990; Soler et al., 1994).

Lotem et al. (1995) showed that egg variability within a clutch of Great Reed Warblers (*Acrocephalus arundinaceus*) was higher in accepter than in rejecter individuals. However, this result was related to the age of hosts, given that younger females were in general worse recognizers and had a higher intra-clutch variation than did older females. Therefore, in the present paper we have also studied the possible relationship between intra-clutch variation and Magpie age, estimated as laying date, due to the fact that young females (one year old) lay later than do older females (Birkhead, 1991).

We studied egg color and pattern using image-analysis computer programs, which for the first time allow a completely objective and detailed assessment of mimicry. We predicted that following the evolutionary-arms-race hypothesis, the probability of Magpie rejection should be (1) inversely related to the degree of Magpie intra-clutch variation and (2) positively related to the degree of difference in color and patterning between the model and Magpie eggs.

Materials and Methods

Description of magpie eggs and clutches

Magpie eggs, subelliptic and shiny, have a typically pale bluish or greenish background with abundant dark brown spots (Alvarez and Arias de Reyna, 1974). It has been shown that magpie eggs vary widely in color, both between and within clutches (Birkhead, 1991). Moreover, there is some evidence that each Magpie female lays distinctively colored eggs (Birkhead, 1991), and that egg size varies within and between populations (Birkhead, 1991).

Study area and natural history

The present work was carried out in the Camargue, southeastern France, a French National Park with a high density of Magpie nests, where Cuckoos at low frequency parasitize some Magpie nests (Frank Cezilly, pers. comm.). The experimental nests were located south of Nimes.

This area is at the northern boundary of the distribution of the Great Spotted Cuckoo, where this species has been breeding for more than a century (Cramp, 1985). Although the Great Spotted Cuckoo is uncommon in this area, the Magpie population has long suffered from parasitism and, thus, we expected some level of egg recognition to have evolved in the population.

The Great Spotted Cuckoo, when laying an egg in a Magpie nest, normally breaks some host eggs, and thus it is difficult to obtain information on the appearance of all Magpie eggs in a parasitized nest (Soler, 1990; Soler et al., 1996). Due to the behavior of the Great Spotted Cuckoo, we chose to test our ideas in the Camargue, an area with a low parasitism rate but with a long period of sympatry. None of the 33 Magpie nests used in the study in the area was parasitized by the Great Spotted Cuckoo, although 25 km west of the Camargue we found two parasitized magpie nests with two cuckoo chicks each. In the Camargue we were able to collect data on all eggs in Magpie clutches and, therefore, we had information on total intra-clutch variation of each experimental Magpie nest.

Experimental model eggs

To test the recognition ability of the magpie population, we used both mimetic and non-mimetic model eggs. We made the mimetic model eggs by filling three different rubber molds of Great Spotted Cuckoo eggs with plaster of Paris. Once dry, the model was removed from the mold and painted with a color similar to the background of the Great Spotted Cuckoo eggs. Later, we painted spots with a distribution, size and color resembling those of real Great Spotted Cuckoo eggs, which are similar to those of the Magpie (see above). Finally, we covered the model eggs with a thin layer of lacquer simulating the sheen of real Cuckoo eggs. Model eggs weighed about the same as those of the Cuckoo (see Soler and Møller, 1990 for more information) and, therefore, model eggs were a close copy of real Cuckoo eggs.

For non-mimetic eggs we used Quail eggs painted red, differing from the Magpie and Great Spotted Cuckoo eggs in size (mean of Magpie eggs volume= 3.16±0.02 cm^3, N=201; mean of mimetic model eggs volume= 2.94±0.06 cm^3, N=14; mean of Quail-egg volume= 4.22±0.11 cm^3, N=16), background color, and spot size and distribution. Each model egg was used only once. The results of one experiment carried out in a Magpie population in southern Spain indicated that Magpies responded identically to non-mimetic model eggs made using plaster of Paris or Quail eggs, both painted red (Soler et al., 1998). In any case, because Quail eggs were painted completely red and, therefore, differed from red plaster of Paris eggs mainly in volume, we introduced the volume both of Magpie and of experimental eggs in the analyses in order to control for this potentially misleading factor.

Experimental design

On finding a Magpie nest containing eggs, we randomly introduced a mimetic or non-mimetic model egg into the nest. We photographed the Magpie eggs together with the model egg on a gray background and returned them to the nest. Between four and six days later, which is the time used in previous studies of Magpie egg recognition, (Soler and Møller, 1990; Soler et al., 1994), we visited the experimental Magpie nest again. When we found more Magpie eggs than during the previous visit, we took another photograph in order to have a visual record of the complete clutch.

On our next visit, we used the term “rejecter” for Magpies that had removed the model egg or abandoned their nest, and “accepter” for Magpies that allowed the model egg to remain in the nest. Several different Magpie responses to the Cuckoo eggs have been described in other areas: abandoning the nest, burying the Cuckoo egg in the nest with new nest material, or ejecting the Cuckoo egg from the nest (M. Soler et al., 1995). In this area, in all cases, the response consisted of ejection of the experimental egg, except for one case in which the Magpie abandoned the nest containing the model egg and one Magpie egg.

In accordance with other studies (Soler and Møller, 1990), there was no significant difference between results of experiments made during the laying period of the host and those made when the last egg had already been laid, either for mimetic (laying period: ejecters= 0, accepters= 4; laying period finished: ejecters= 2, accepters= 8; Fisher exact test, P=1) or non-mimetic model eggs (laying period: ejecters= 5, accepters= 1; laying period finished: ejectors= 5, accepters= 5; Fisher exact test, P=0.31). Therefore, we pooled the results of all nests regardless of when the experiments were made. We used each nest only once.

We conducted 33 experiments, but two nests were depredated and one abandoned (see above) before we were able to obtain data on the appearance of the complete Magpie clutch. We removed these three nests from the analyses. Thus, we considered 14 tests with mimetic eggs and 16 with non-mimetic eggs. There was no significant differences between mimetic and non-mimetic experimental nests in breeding parameters (laying date, clutch size, number of nestlings in the nest, fledgling success, size of the Magpie nest) or egg-appearance variables (mean egg volume, mean egg color, egg intra-clutch variation in color, mean spot variation and intra-clutch variation in spots); (for explanation of the egg appearance variables, see the section below entitled “Variables used in the analysis”). Therefore, the experimental nests represented unbiased samples.

Photograph analyses

We took photos of Magpie eggs using 100 ASA color Kodak film. For each photo, we placed the eggs on a Kodak neutral-gray card, which reflects 18% of the light falling on it and also has a protective lacquer coating that reduces reflectance. In this way, we had a neutral background which did not affect the light or the final color of the pictures. We also placed a Kodak color control patch below the eggs in each photo to compare the color of the eggs with this known printing color. This enabled us to correct for color changes due to different light conditions.

In the laboratory, we first scanned the pictures with a resolution of 140 pixels per inch and later used the Adobe Photoshop computer program (version 2.5.1) to analyze the hues of the red, blue and green Kodak control color patches. Any color on the computer screen is defined by three different values corresponding to the three different channels: blue, green and red. The values vary from zero (no color at all in the channel) to 255 corresponding to a completely saturated color (i.e., in a color photograph, black corresponds to a value 0 for the blue, green and red channels, while white would have the maximum value in all three channels).

We measured the hue of the red, green and blue Kodak patches on the red, green and blue channels, respectively. We calculated the mean value for all the photos used in the analysis for the three color patches and used the residual of the mean value to correct egg color values of the three different channels. In other words, we added to the color values of the eggs in one photo the signed differences between the hue of the red, green and blue Kodak patches on the red, green and blue channels, respectively, and the mean value for all photos. In so doing, we controlled the color values for differences in light conditions under which the photos were taken.

Afterwards, we split each image into three different channels (blue, green and red) producing a black and white photograph where the values of each channel were transformed to values of gray scales, and we used the NIH-Image program (Rasband, 1994) to analyze the three channels of the Magpie eggs.

For each image, we measured the color in three different sections of the eggs. We calculated the mean and variance, in the three different channels in pixel-color intensity inside an ellipse corresponding to three different sections of the eggs: one in the center, another towards the narrower end of the egg and another towards in the broader end of the egg. The size of each ellipse was approximately one fourth of the entire elliptical area of the egg avoiding reflecting parts. Therefore, we took three measurements per egg for each channel; that is, nine mean and variance values of color from each egg. Later, we corrected those mean values by subtracting the residual value of the Kodak color control patches for each channel (see above).

Because Magpie eggs from different clutches have similar color patterns of eggs, we found a strong correlation between the different channels, both in mean color values of each section of the egg (between blue and green, r=0.97; between blue and red, r=0.88; between green and red, r=0.90; N =684 (three different part of the 228 eggs), P< 0.0001) as well as in variance of the color pixels of the egg (between blue and green, r=0.92; between blue and red, r=0.73; between green and red, r=0.78; N=684 (three different part of the 228), P<0.0001). Therefore, we performed a Principal Component Analysis (PCA) that resulted in two axes, one related to the mean color values and the other to the variance of the pixel color of the egg, which explained 52% and 41% of the total variance, respectively. Therefore, due to the strong correlation between channels, Magpie egg color differed mainly in darkness we used the coordinates of these PCA axes as values of egg- color and the egg-color variation.

Variables used in the analyses

(a) Nest volume were used as an indicator of the parental quality of Magpie pairs (J.J. Soler et al., 1995), calculated by the equation for an ellipsoid, since Magpies build domed nests:

$$\text{Nest volume} = 4/3\ \pi\ r^2\ R$$

where “r” is the shortest radius and “R” is the longest radius of the nest measured in the field to the nearest 1mm. We standardized the nest volume in order to have the same amount of variance as in other variables in the logistic regression analysis.

(b) Mean volume of eggs in the clutch: we calculated the egg volume from the equation:

$$\text{Vol} = 4/3\ \pi\ r^2\ R$$

where “r” is the transverse radius and “R” is the longitudinal radius measured in the field with a caliper to the nearest 0.01mm. We standardized egg volume, again, in order to have the same amount of variance as in other variables in the logistic regression analysis.

(c) Intra-clutch variation in egg volume: as the variance of the egg volume in the clutch. We also standardized

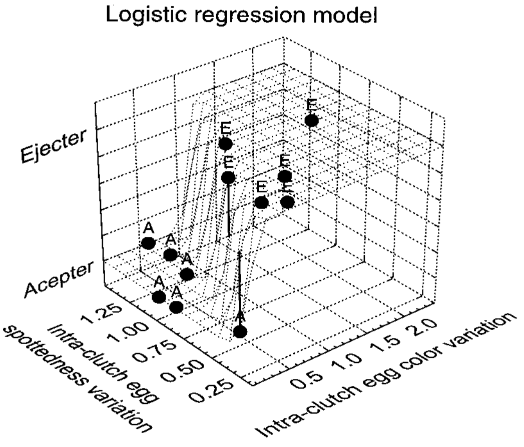

Figure 1.- Relationship between intra-clutch variation in spots and color and the ejection of non-mimetic eggs by the Magpie. Logistic regression model (*2 log (likelihood)*=4.61, χ^2=16.56, *d.f.*=2, P<0.0005).

Table 1. Parameters of Magpie eggs for ejecter and accepter nests exposed to mimetic and non-mimetic model eggs.

	Accepters	Ejecters
	Mean± SE (N)	Mean±SE (N)
Mimetic-egg experiments		
Nest volume (cm³)	30017.57 ± 3713.49 (12)	14940.00 ± 9825.96 (2)
Egg volume (mm³)	3144.92 ± 69.41 (12)	2995.99 ± 222.76 (2)
Egg volume intra-clutch variation	25883.36 ± 11200.05 (12)	8976.94 ± 10497.53 (2)
Egg color	0.05 ± 0.17 (12)	0.08 ± 0.64 (2)
Egg color intra-clutch variation	0.49 ± 0.14 (12)	0.39 ± 0.40 (2)
Egg spots	0.04 ± 0.23 (12)	0.50 ± 0.41 (2)
Egg spots intra-clutch variation	0.67 ± 0.13 (12)	0.46 ± 0.11 (2)
Difference in color between Magpie and model egg	-1.37 ± 0.18 (12)	0.21 ± 2.24 (2)
Difference in spots between Magpie and model egg	-0.06 ± 0.26 (12)	0.99 ± 1.12 (2)
Non-mimetic-egg experiments		
Nest volume (cm³)	22154.93 ± 4420.12 (5)	14940.00 ± 3403.53 (8)
Egg volume (mm³)	3185.13 ± 156.79 (6)	3208.30 ± 54.46 (10)
Egg volume intra-clutch variation	33350.08 ± 14853.60 (6)	15719.09 ± 5005.22 (10)
Egg color	-0.36 ± 0.34 (6)	0.04 ± 0.16 (10)
Egg color intra-clutch variation	0.36 ± 0.12 (6)	0.83 ± 0.24 (10)
Egg spots	0.16 ± 0.24 (6)	0.10 ± 0.24 (10)
Egg spots intra-clutch variation	1.01 ± 0.17 (6)	0.57 ± 0.13 (10)
Difference in color between Magpie and model egg	0.59 ± 0.23 (6)	0.86 ± 0.17 (10)
Difference in spots between Magpie and model egg	1.71 ± 0.29 (6)	1.48 ± 0.28 (10)

intra-clutch variation in egg volume in order to have the same amount of variance as in other variables.

(d) Mean egg color in the clutch: as the mean of the hue of the three different sections of the eggs in the clutch. Although this value is the mean color of both background and spots, because the Magpie and Great Spotted Cuckoo (mimetic model) eggs are similar in the color of both background and spots (see above), changes in this variable reflect change in the egg coloration. In addition, this variable enables us to distinguish between non-mimetic model eggs and Magpie or mimetic model eggs.

(e) Intra-clutch variation in color: as the addition of the intra-clutch variation in egg color of each section of the egg (see above).

(f) Degree of spottedness in the clutch: we estimated the degree of spottiness by using the variance of the hue of the pixel measured on the eggs. Because the Magpie and Great Spotted Cuckoo (mimetic model) eggs are similar in background and spots color (see above), great amounts of variation indicate that there was high variability of colors on the eggs and therefore a great amount of spots. The highest value of this variable was obtained when the area with spots equaled the area without spots. Thus we calculated the mean value of the clutch from the three parts of the eggs.

(g) Intra-clutch variation in the degree of spottedness: as the addition of intra-clutch variation in the level of spottedness of each section of the eggs.

(h) Difference in color between Magpie eggs and the experimental egg: as the difference between variable (d) and the value of the color of the experimental model egg introduced into the Magpie nest.

(i) Difference in the level of spottedness between Magpie eggs and experimental egg: as the difference between variable (f) and the value of the spottedness of the model egg.

Statistical procedures

We used each nest as an independent observation and only for one type of experiment (mimetic or non-mimetic model egg). We used a log-linear regression model to investigate which egg variables best explained ejection or acceptance of experimental eggs. Whether a model egg was ejected or accepted was used as the binary dependent variable and all egg variables in the clutch were the independent variables. As the dependent variable has a binomial rather than normal distribution, we used the maximum-likelihood method (Sokal and Rohlf, 1995). All statistical tests were two tailed. Values are mean ± SE.

Results

Ejection rate in the magpie population

According to previous experiments (Soler and Møller, 1990; Soler et al., 1994), the level of recognition in the Magpie population was higher for non-mimetic than for mimetic eggs. From 16 non-mimetic experimental nests, 6 (37.5%) incubated the non-mimetic model eggs, while 12 of 14 (85.7%) of the mimetic model eggs were incubated ($\chi^2=7.73$, d.f.=1, $p<0.006$).

Is the appearance of magpie eggs related to the probability of ejection of non-mimetic eggs?

The mean values for all variables analyzed are shown in Table 1. Confirming the first prediction, we found that the variables indicative of intra-clutch variation were those most closely related with the probability of magpie ejection behavior. That is, ejecters had generally lower mean values in intra-clutch variation variables than did accepters (Table 1).

Table 2. Differences in proportion of variance explained by the logistic regression model with rejection behavior as a dependent variable (rejecter or accepter), and intra-clutch variation in egg color and spots as independent variables from the non-mimetic-egg experiments and the logistic regression model introducing other variables.

	Difference	d.f.	P
Nest volume (cm³)	0.131	3	0.72
Egg volume (mm³)	4.480	3	0.03
Egg volume variation[1]	0.131	3	0.72
Egg color	0.073	3	0.79
Egg spots	0.130	3	0.72
Difference in color[2]	0.117	3	0.73
Difference in spots[2]	0.022	3	0.88

[1] Intraclutch variation in egg volume

[2] Difference between Magpie and model egg

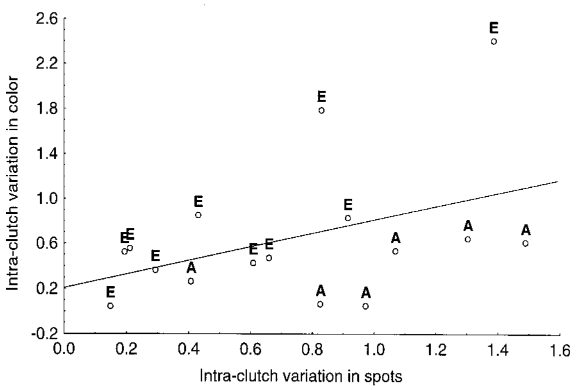

Figure 2.- Relationship between intra-clutch variation in spots and color of the Magpie clutches. **E** = ejecter and **A** = accepter.

The intra-clutch variation in spottiness and color were the two variables that best explained the probability of ejection of non-mimetic model eggs (logistic regression model, maximum likelihood $\chi^2=16.6$, d.f.=2, $p<0.0005$; Fig. 1). Egg volume significantly improved the predictive power of these two variables (Table 2). Moreover, these two intra-clutch variables correctly classified 100% of the ejecter and 83% of the accepter nests in a discriminant analysis (Wilks' Lambda=0.33, p=0.001).

However, intra-clutch variation in color was related to ejection in the opposite direction than predicted; nests with smaller intra-clutch variation in color accepted the non-mimetic eggs, while, in accordance with the prediction, nests with lower intra-clutch variation in spots better discriminated against non-mimetic eggs. This intra-clutch variation was the first in the stepwise discriminant analysis (first step, intra-clutch variation in spots, Wilks' Lambda=0.86, $p<0.0005$). In any case, most ejecter nests had small intra-clutch variation in spottedness and intra-clutch variation in color (Fig. 2).

Is the appearance of magpie eggs related to the probability of ejection of mimetic eggs?

Only two magpies of 14 ejected the mimetic model eggs; thus, although the statistical power of the analysis is not high the results may be informative. The mean values of each variable for accepters and ejecters are listed in Table 1. In this case, following the predictions, the difference in color between model and real Magpie eggs was the variable that best explained the results of the experiment. We found that the intra-clutch variation in egg volume significantly improved the predictability of the model with the differences in color (differences with the model=4.15, number of parameters=2, $p<0.05$; logistic regression model, maximum likelihood $\chi^2=7.77$, d.f.=2, $p<0.03$). No other variables improved the model.

The difference in color between model and real Magpie eggs discriminated significantly between the eggs of ejecters and accepters (Wilks' Lambda=0.68, $p<0.05$) and correctly classified 93% of the cases.

Is the appearance of magpie eggs related to the magpie age?

Intra-clutch variation in egg appearance was unrelated to the time of breeding, which related to Magpie age (Birkhead, 1991), for all variables: spottedness variation (Spearman rank correlation, r=0.11, p>0.5), color variation (Spearman rank correlation, r=0.25, p>0.15) and volume variation (Spearman rank correlation, r=-0.09, p>0.5).

Discussion

Host egg recognition and cuckoo egg mimicry are based on a visual mechanism in the host as well as in the human observer detecting the mimicry. However, the visual capacity of the host is not the same as that of the observer and ignoring this fact could result in fundamental errors in scientific analisys. With respect to visual capacity, birds often surpass humans in color vision; most species possess four or even five cone pigments in their retina and many species can see in the ultraviolet (UV) spectral range (Martin, 1995, see also Bennett et al., 1994).

Experiments based on human perception would tend to underestimate the degree of difference between cuckoo and host eggs and therefore overestimate mimicry between the eggs of the cuckoo and those of the host. However, the results presented here appear to be valid because Magpies respond to color variation in model eggs, and many species of brood parasites mimic the color of host eggs in the range of human spectral vision. Moreover, it has been shown repeatedly that host bird species respond to variation of mimicry in this spectral range.

Lotem et al. (1995) showed that egg variability within a clutch of Great Reed Warblers was related to the age of hosts, given that younger females had higher intra-clutch variation than did older females and, therefore, younger females were in general worse

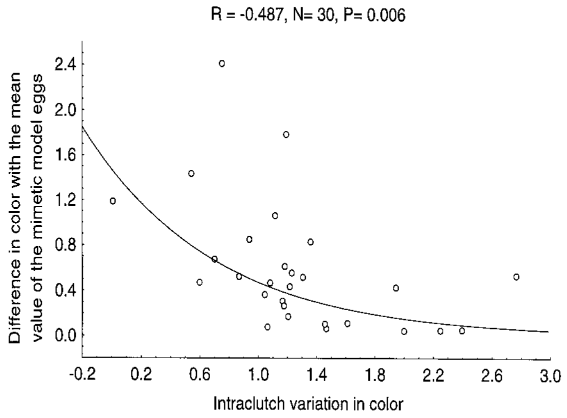

Figure 3.- Relationship between the intra-clutch variation of Magpie eggs and the difference between mean value of the color of Magpie eggs and the mean value of the mimetic eggs.

recognizers. However, when the rejection rate was corrected for the age of the host, clutches of rejecters tended to be more variable than those of accepters, contrary to the predictions by Lotem et al. (1995). In the Magpie, intra-clutch variation in egg appearance was unrelated to the time of breeding which is related to the Magpie age (Birkhead, 1991). Therefore, in the Magpie, the recognition ability appears not to be related to the age of the bird.

Although the sample size is small, we found that intra-clutch variation in spottedness explained the ability of the Magpie to eject non-mimetic model eggs, but not the intra-clutch variation in color and, therefore egg spottedness is apparently more important for the general appearance of the eggs. In accordance with the evolutionary arms race theory of brood parasitism (Øien et al., 1995; Soler and Møller, 1996), Magpies having clutches with a small degree of variation ejected non-mimetic model eggs more often. Therefore, in the Magpie, only intrinsic characteristics of clutches were necessary to explain ejection behavior of non mimetic model eggs.

These characteristics could have evolved not only as a response to interspecific brood parasitism, but also to intraspecific brood parasitism (Møller and Petrie 1990). The level of intraspecific parasitism depends on different ecological factors such as population density (Møller and Petrie 1990). Although it is probable that Magpie egg recognition has evolved in response to parasitism by the Great Spotted Cuckoo (Soler 1990, Soler and Møller 1990), experiments in other areas with different levels of interspecific brood parasitism should be done in order to clarify the selection pressures affecting intra-clutch variation in areas of sympatry with the Great Spotted Cuckoo.

In experiments with mimetic model eggs, although intra-clutch variation in egg volume was influential, the difference between the model and the Magpie egg was more relevant than the intrinsic characteristics of the Magpie clutch. This result is important because a reduction of these differences would be selectively advantageous for the brood parasite and, thus, this could be the selective pressure forcing the brood parasite to mimic the host eggs. Although, previously, it has been shown that different experimental model eggs, painted with different colors, provoke on the host different responses (acceptance or rejection) (e.g. Brooke and Davies 1988, Davies and Brooke 1988, 1989a, Soler et al. 1994), this study is the first showing that, using the same kind of model egg (mimetic), small differences in mimicry provoke different responses of the host acceptance or ejection of model eggs in accordance with the evolutionary-arms-race hypothesis between parasite and host (Dawkins and Krebs 1979).

Although the Great Spotted Cuckoo lays eggs very similar to Magpie eggs in color and spottedness (Alvarez et al. 1976, Birkhead 1991, Soler 1990), it is unclear whether this similarity has resulted from an evolutionary Cuckoo response to Magpie ejection behavior, or from an ancestral Cuckoo trait preceding the use of Magpies as a host. According to the data available, it is most likely that the eggs of the Magpie and the Great Spotted Cuckoo were similar before the cuckoo started to use the Magpie as a host. This likelihood is supported by the fact that, regardless of the hosts parasitized in Europe, the color and spot patterns of Great Spotted Cuckoo eggs are similar (Soler 1990). This constancy is true even for the sub-Saharan African Great Spotted Cuckoo population. In this area, the great spotted cuckoo parasitizes other corvid species, starlings and hoopoes (Fry et al. 1988), despite more pronounced differences in egg size and color patterns than between Cuckoos and Magpies (Friedman, 1948).

If the similarity between the eggs of Magpies and Great Spotted Cuckoos existed before these two species became sympatric, the coloration of the Magpie eggs could have evolved not only by reducing intra-clutch variation, but also increasing differences from those of the cuckoo. This is the second step described by Øien et al. (1995, see also Soler and Møller 1996) in the evolution of the egg appearance of hosts suffering from brood parasites that mimic host eggs. This step consists of the increased inter-clutch variation among hosts, thereby making parasite egg mimicry more difficult.

The evolutionary mechanism of increased inter-clutch variation could be particularly important in the Great Spotted Cuckoo and the Magpie, where the Cuckoo does not apparently modify the appearance of its eggs. Therefore, if the appearance of the Great Spotted Cuckoo eggs are not able to evolve with the appearance of the host eggs, it would be selectively advantageous for the Magpie to lay eggs differing from those of the Great Spotted Cuckoo. Thus, Magpies that recognize Cuckoo eggs should lay the most dissimilar eggs from those of the Cuckoo, but also reduce intra-clutch variation. In support of this prediction, we found a significant negative relationship between the intra-clutch variation in color and the degree of difference between Magpie eggs and the mean of mimetic model eggs (Fig. 3).

In conclusion, we have shown that intrinsic characteristics of Magpie eggs alone can explain the recognition of non-mimetic eggs. When the model egg mimics the Magpie eggs, the characteristics of this model egg differing from the Magpie eggs allow the Magpie to recognize and reject the models, in agreement with the contention that egg ejection by the host is a selection pressure for the parasite mimicking host eggs. However, the experimental results indicate that egg recognition not only is related to the intrinsic characteristics of host eggs but also depends on small levels of change in the degree of mimicry of parasitic eggs, in accordance with the idea that egg recognition by the host is a selection pressure for the evolution of mimicry in brood-parasite eggs.

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